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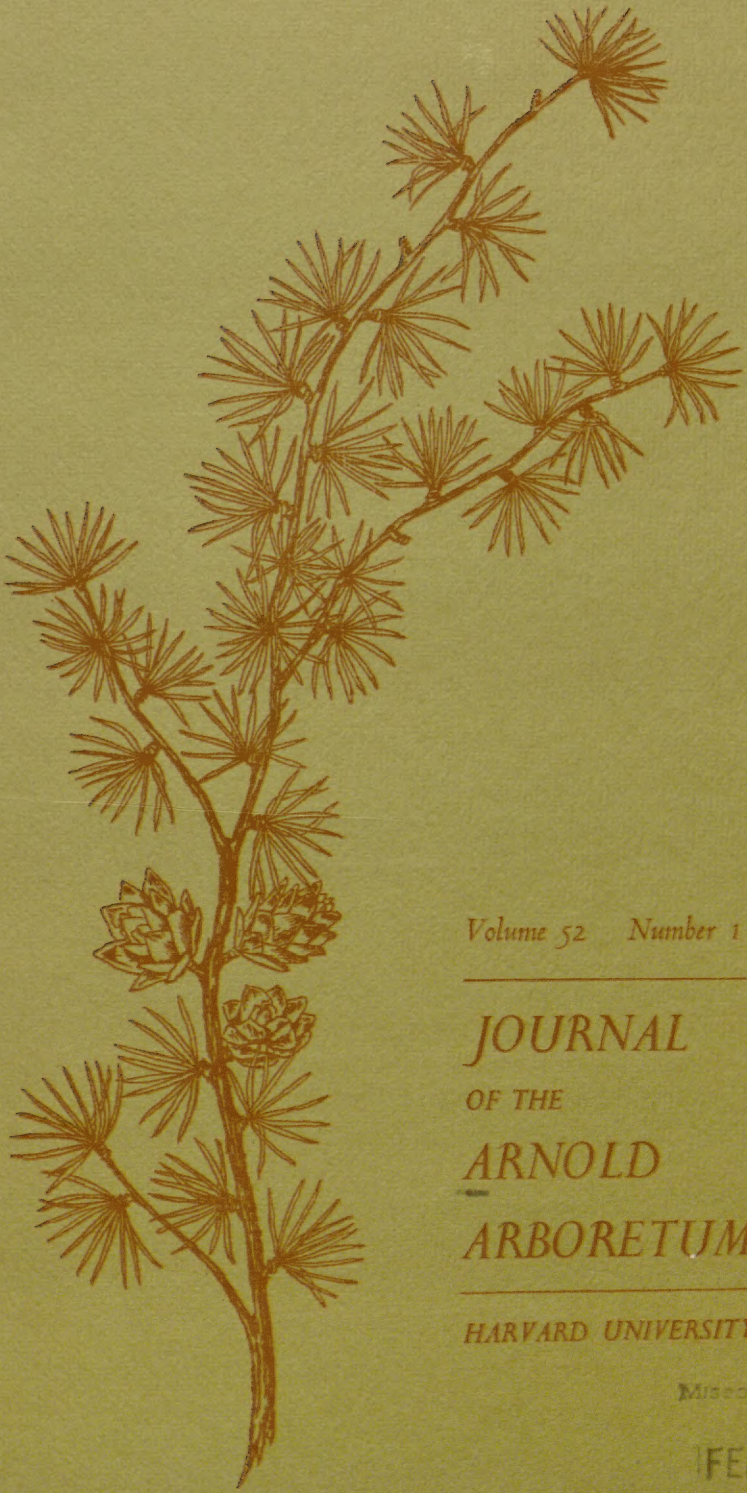

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EMBRYOLOGY OF THE MAGNOLIALES AND COMMENTS ON THEIR RELATIONSHIPS [1]

N. N. BHANDARI

EVER SINCE THE PROPOSAL of Bennettitalian origin of angiosperms, the magnolian complex and particularly the Magnoliaceae, have occupied a pivotal position in all phylogenetic considerations, since in the "Magnolia flower" the proponents of this theory visualized all the representative analogous reproductive parts in the Bennettitalian fructification.

No doubt the various theories to interpret the angiosperm flower and its appendages, such as the telome theory (*see* Zimmermann, 1955; Wilson, 1937, 1942, 1953; Wilson & Just, 1939), gonophyll theory (Melville, 1962, 1963) and interpretation of the angiosperm flower (Barnard, 1961; Sporne, 1949) are exhaustive mental exercises based directly on the extinct plants. However, the fast emerging fact is that the living ranalian members should be subjected to an extensive survey from all points of view, in order to understand, if not the origin of the angiosperms, at least the basic primitive patterns and their further diversifications during the course of phylogeny. Consequently, this resulted in a concerted effort to investigate fully the morphology, anatomy, and embryology of this interesting group of the dicotyledons.

It is rather fortunate that the group attracted the attention of two doyens of plant morphology and embryology, Professor I. W. Bailey and Professor P. Maheshwari, who established strong schools in their respective fields to gain an insight into the ranalian complex. By coordinated effort over a span of 30 years or more Professor I. W. Bailey and his colleagues have projected explicitly the basic primitive morphological and anatomical patterns and their amplification, in ascending or descending phylogenetic series, in numerous ranalian families. Their efforts have resulted in studies on the Magnoliaceae (Canright, 1952a,b; 1955; 1960; 1965), Degeneriaceae (Bailey & Smith, 1942; Swamy, 1949), Winteraceae (Bailey, 1944b; Bailey & Nast, 1943a,b; 1944a,b; 1945; Nast, 1944), Himantandraceae (Bailey, Nast, & Smith, 1943), Schisandraceae

[1] Dedicated to the memory of the late Professor P. Maheshwari, a renowned embryologist and my teacher, and the late Professor I. W. Bailey, a great plant anatomist and morphologist.

and Illiciaceae (Bailey & Nast, 1948; Smith, 1947), Austrobaileyaceae (Bailey & Swamy, 1949), Trimeniaceae and Monimiaceae (Money, Bailey, & Swamy, 1950), Amborellaceae (Bailey, 1947; Bailey & Swamy, 1948), Gomortegaceae (Money, Bailey, & Swamy, 1950), Trochodendraceae and Tetracentraceae (Bailey & Thompson, 1918; Bailey & Nast, 1945; Nast & Bailey, 1945; Smith, 1945), Eupteleaceae (Nast & Bailey, 1946; Smith, 1946), and Cercidiphyllaceae (Bailey & Nast, 1945; Nast & Bailey, 1945; Swamy & Bailey, 1949).

On the other hand, Professor P. Maheshwari interested some of his pupils in taking up a study of the embryology of some ranalian families. They have contributed substantially towards our knowledge of such families as the Magnoliaceae (Bhandari, 1967a; Kapil & Bhandari, 1964), Degeneriaceae (Bhandari, 1967b), Himantandraceae (Vijayaraghavan & Bhandari, 1970), Winteraceae (Bhandari, 1963b, 1967c; Bhandari & Venkataraman, 1968), Myristicaceae (Bhandari, 1967d), Canellaceae (Bhandari, 1967e), Schisandraceae (Bhandari, 1967f; Jalan & Bhandari, 1963; Jalan & Kapil, 1965; Kapil & Jalan, 1964), Illiciaceae (Bhandari, 1967g), Monimiaceae (Bhandari, 1967h), Calycanthaceae (Bhandari, 1967i), Lauraceae (Bhandari, 1967j), Trochodendraceae (Bhandari, 1967k), Cercidiphyllaceae (Bhandari, 1967l), Chloranthaceae (Vijayaraghavan, 1964), and Ranunculaceae (Bhandari, 1962, 1963a, 1965, 1966, 1968; Bhandari & Asnani, 1968; Bhandari & Kapil, 1964; Bhandari & Vijayaraghavan, 1970; Jalan, 1963; Jalan & Bhandari, 1963; Kapil & Jalan, 1962; Vijayaraghavan, 1962, 1963; Vijayaraghavan & Bhandari, 1970; Vijayaraghavan & Marwaha, 1969a,b).

Erdtman (1952), Erdtman & Metcalfe (1963), and Wodehouse (1935, 1936) have contributed immensely towards the study of pollen morphology and its application in systematics. Pollen characters no doubt form one of the fundamental features in considering interrelationships amongst various families and must be fully utilized.

The chromosome number and the karyotypic studies can be very meaningful in considering interrelationship within this interesting group. Unfortunately, as compared to the large number of taxa included in this order, chromosome numbers for only a few of them have been worked out. Furthermore, as pointed out by Raven and Kyhos (1965), the chromosome counts for not even a single species of one of the primitive families, the Winteraceae, as summarized by Darlington and Wylie (1955) stands correct today. This fact stresses the need for rechecking of the basic number reported during the 1930's. As pointed out earlier, karyotype might have an important bearing on the interrelationship amongst the various primitive families. Such precise studies are wanting; however, recent investigations by Rüdenberg (1967), Stone (1968), and Stone and Freeman (1968) are welcome additions.

It is fully realized that although it is not possible to erect a phylogenetic system of classification based on embryological characters alone, it is also not tenable with any other single series of characters. However, that the embryological characters play an important role in deciding the inter-

relationships in particular instances has been amply emphasized by Maheshwari (1950a,b, 1954, 1956, 1959, 1963, 1964), Johri (1963), Kapil (1962), Subramanyam (1962), and Cave (1959). Therefore, an attempt like the present one to tabulate and evaluate the embryological evidences in conjunction with others in phylogenetic considerations of the Magnoliales needs no justification.

The order Ranales *sensu lato* has undergone tremendous changes because of the injunction of phylogeny in taxonomy (Cronquist, 1968; Engler, 1964; Takhtajan, 1966; Thorne, 1968) and there have been many additions or deletions from one family to another and *vice versa*. Furthermore, a large number of taxa have been excluded from or included in this group by one or the other taxonomist. In this review I have followed the recently proposed system by Cronquist (1968) which includes 19 families in the order Magnoliales, comprising chiefly the woody members of the ranalian complex.

The families Trochodendraceae and Cercidiphyllaceae have also been included although these along with Tetracentraceae and Eupteleaceae are placed in the orders Trochodendrales and Hamamelidales. This system (Cronquist, 1968) has been followed only to have a framework for the review without giving due consideration to any of its phylogenetic implications. Embryological information on Lactoridaceae, Eupomatiaceae, Trimeniaceae, Amborellaceae, Gomortegaceae, Hernandiaceae, Tetracentraceae and Eupteleaceae is wanting. These have, therefore, been excluded from the description of the families, but since well established relationships have been shown based chiefly on the morphological and anatomical evidence I have included some of these families in the discussion on interrelationships of the Magnoliales in order to make the evaluation as complete as possible.

EMBRYOLOGY AND CYTOLOGY

Austrobaileyaceae. The family comprises a single genus, *Austrobaileya*, with two species distributed in Australia. Embryological information is meager and according to Davis (1966) is unknown; perhaps she overlooked the passing reference made by Bailey and Swamy (1949) concerning some points in the anther wall development and male gametophyte. The wall of the young microsporangium comprises the epidermis, three wall layers, and an irregularly two-layered glandular tapetum having binucleate cells. At maturity the epidermal cells become protuberant, the endothecial cells enlarge but it could not be made out from the illustrations whether these develop characteristic fibrous bands or not. The middle layers and the tapetum become absorbed and only their remnants are perceptible. Cytokinesis is simultaneous. As in *Degeneria* the exine formation begins while the microspores are still in tetrads. The germinal furrow develops along the distal face where also the generative cell is cut off. The mature pollen is spherical, monocolpate with colpus extending from one pole to the other; the exine is finely pitted. The external

surface of the furrow possesses minute protuberances. Rüdenberg (1967) has investigated the karyotype of *Austrobaileya* and found $2n = 44$. The basic number in the family would be $x = 22$.

Magnoliaceae. The Magnoliaceae are distributed primarly in eastern Asia, Malesia, southeastern North America, Central America, the West Indies, and Brazil. In India the family is represented by 22 species belonging to 5 genera. Embryological literature concerns only *Magnolia* (Brandza, 1891; Earle, 1938a,b; Farr, 1918; Hayashi, 1960, 1964; Kapil & Bhandari, 1964), *Michelia* (Padmanabhan, 1960) and *Liriodendron* (Kaeiser & Boyce, 1962).

The anther wall at the microspore mother cell stage comprises the epidermis, endothecium, 3 or 4 middle layers and bilayered glandular tapetum (FIGURE 1 A). By the time the cytokinesis is completed in the microspore mother cells, a large number of Ubisch granules line the inner walls of the tapetum. In a fully mature anther the papillate epidermis and endothecium along with 2 or 3 middle layers persist (FIGURE 1 B). In *Magnolia stellata* (Kapil & Bhandari, 1964) the endothecium possesses reticulate thickenings instead of the usual fibrous bands found in other members. After meiosis II in the microspore mother cells the cytokinesis takes place by furrowing (FIGURES 1 C, D), resulting in tetrahedral or isobilateral tetrads (FIGURE 1 E). The mature pollen is monocolpate (FIGURE 1 G) and is shed at the 2-celled stage (FIGURE 1 F). The generative cell is surrounded by a thin sheath of finely granular cytoplasm and a delicate membrane (FIGURE 1 F).

The number of ovules in a carpel varies from 6 to 2 in different genera. They are anatropous, bitegmic, and crassinucellate; the outer integument is vascularized. The hypodermal archesporium is multicellular (FIGURE 1 H) although ultimately only one cell functions. The primary parietal cell divides repeatedly to form the parietal tissue so that the megaspore mother cell is buried deep in the nucellus. At the end of meiosis II linear or T-shaped megaspore tetrads are formed (FIGURES 1 I, J). The chalazal megaspore functions giving rise to the Polygonum type of embryo sac (FIGURE 1 K). The synergids and antipodal cells are ephemeral.

The development of the endosperm is *ab initio* cellular. The first division is transverse and the two chambers thus resulting contribute to the endosperm proper. In *Magnolia obovata* (Kapil & Bhandari, 1964), however, the chalazal chamber gives rise to a 2- or 3-celled haustorium (FIGURE 1 L). The chalazal haustorium is active until the endosperm proper is well developed, but in the ripe seed becomes completely crushed (FIGURE 1 M). The division of the zygote is transverse, obliquely transverse, or vertical (Kapil & Bhandari, 1964). The embryogeny is either irregular or follows the Onagrad type. The mature embryo is dicotyledonous with a prominent suspensor.

The seed coat is organized chiefly from the outer integument while the inner integument is represented by a layer of crushed cells (FIGURE 1 M). In a ripe seed the testa consists of an outer fleshy region comprising (1)

epidermis of the outer integument, (2) 2 or 3 layers of tangentially elongated cells, (3) a 10- to 12-layered fleshy zone, (4) 2 or 3 layers of tangentially compressed cells, and an inner stony region of 3 or 4 layers of lignified cells.

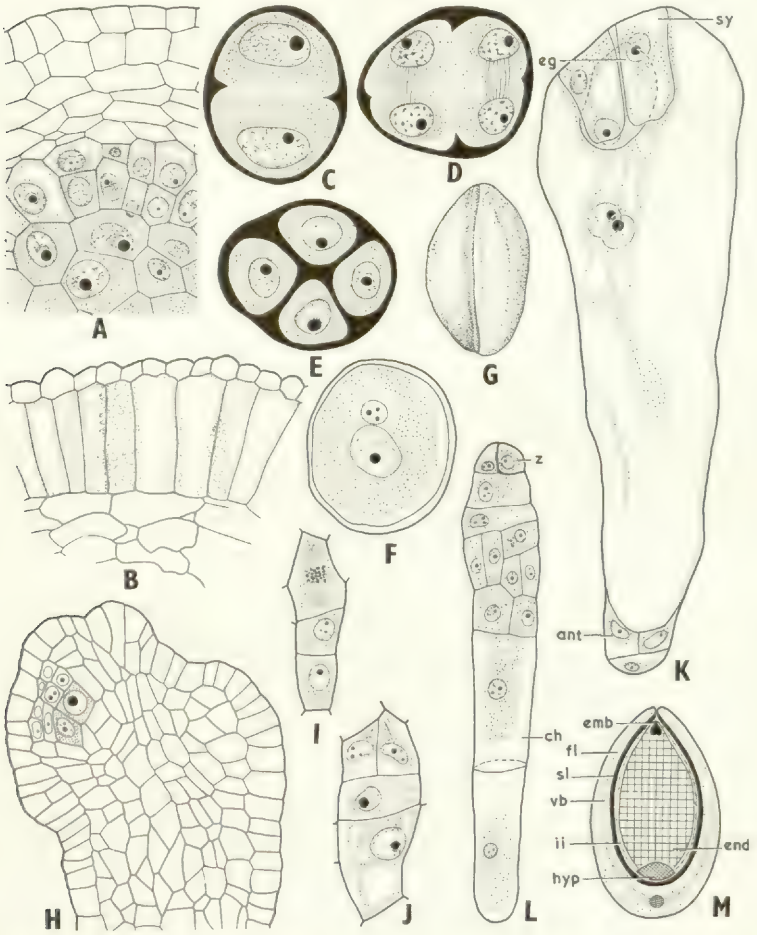

FIGURE 1. **Magnoliaceae.** (*ant*, antipodal cells; *ch*, chalazal haustorium; *eg*, egg; *emb*, embryo; *end*, endosperm; *fl*, fleshy layer; *hyp*, hypostase; *ii*, inner integument; *sl*, stony layer; *sy*, synergid; *vb*, vascular bundle; *z*, zygote.) A, Transection of a part of the anther lobe showing the wall layers, bilayered tapetum and sporogenous tissue. B, Same, showing reticulate thickening in the endothecium. C–E, Stages in microsporogenesis; cytokinesis occurs by furrowing. F, Two-celled pollen. G, Palynogram. H, Longisection of ovule showing parietal layers, sporogenous tissue and initiation of the two integuments. I, J, Linear and T-shaped tetrads of megaspores. K, Organized embryo sac. L, Thirteen-celled endosperm; chalazal haustorium is two-celled. M, Longitudinal section of seed showing various zones of testa; chalazal haustorium has degenerated. (A–M, *Magnolia*, after Kapil & Bhandari, 1964.)

A number of stomata of the haplocheilic type develop on the epidermis of the outer integument (*see* Paliwal & Bhandari, 1962).

Cytological investigations (*see* Darlington & Wylie, 1955; Nanda, 1962; Raven, 1967) concern *Liriodendron* (2 spp.), *Manglietia* (2 spp.), *Michelia* (7 spp.), *Pachylarnax phiocarpa, Talauma hodgsoni* and *T. phellocarpa,* and *Magnolia* (39 spp.). The basic chromosome number is x = 19. Polyploidy is reported in *Magnolia* which includes 4 tetraploid, 11 hexaploid, 1 pentaploid and 1 triploid species. Janaki Ammal (1953) reported $2n = 95$ in *M. soulangeana* whereas Nanda (1962) observed $n = 38$. If the identification of both the plants is dependable, then this is the only record of intraspecific cytological forms. Whatever the origin of basic number, polyploidy seems to have played some role in speciation in *Magnolia*, whereas the chief differences in the genomes seems to have occurred at the gene level within various genera.

Winteraceae. Six vesselless genera with about 95 species comprise the family Winteraceae which is distributed in the tropical and subtropical regions of the world. Three genera are endemic (*Pseudowintera* in New Zealand, *Exospermum* and *Zygonum* in New Caledonia), the other three genera (*Drimys, Bubbia,* and *Belliolum*) occur in New Caledonia, New Guinea, eastern Australia, and Central and South America.

The family is of interest because of the presence of a number of primitive characters such as the undifferentiated stamens with protruding connective tissue (*Belliolum*), a conduplicate sessile or stipitate carpel, stigmatic crest, laminar placentation and primitive vesselless xylem. Morphology and anatomy have received adequate attention at the hands of Bailey (1944), Bailey and Nast (1943a,b; 1944a,b; 1945), and Nast (1944). The embryological investigations, however, are restricted to three genera, *Drimys* (Bhandari & Venkataraman, 1968; Kutti Amma, 1938; Strasburger, 1905), *Pseudowintera* (Bhandari, 1963; Sampson, 1963), and *Zygogynum* (Swamy, 1952).

Four groups of archesporial cells (FIGURE 2 A) differentiate in a young anther. The hypodermal layer divides periclinally to form the primary parietal layer and the sporogenous layer; the others, however, add directly to the sporogenous tissue (FIGURE 2 B). The anther wall comprises epidermis, fibrous endothecium, 2 to 4 middle layers and glandular (*Drimys winteri, Pseudowintera axillaris, Zygogynum*) or amoeboid tapetum (*Pseudowintera colorata*) of parietal origin (FIGURES 2 C, D). The fibrous bands like that of the endothecium extend to 2 or 3 layers of the connective tissue. In *Zygogynum baillonii*, after meiosis is completed in the microspore mother cells, simultaneous cytokinesis results in tetrahedral or decussate tetrads (FIGURES 2 E–H). In *Drimys* and *Pseudowintera* the microspores in the same tetrad show different stages during the formation of the generative cell which is cut off towards the proximal end (FIGURE 2 H), whereas in *Zygogynum* the division is synchronous (FIGURE 2 G). The pollen grains are monoporate; the pore develops at the distal end. The intine is thick and protrudes through the pore. The grains are shed

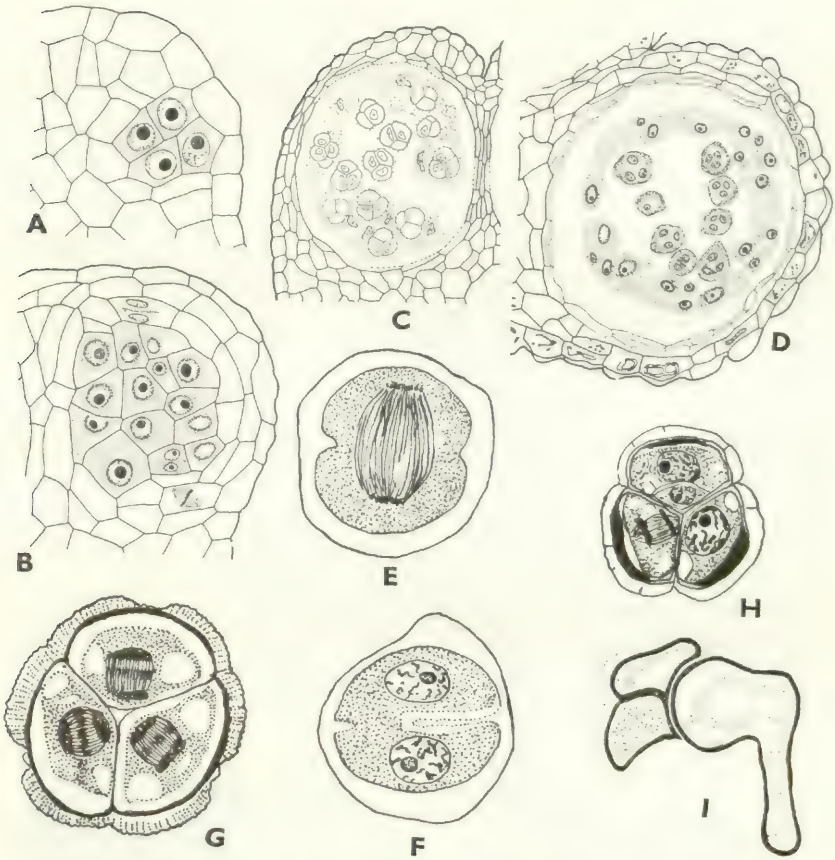

FIGURE 2. **Winteraceae.** A, Transection of anther showing archesporium. B, Representation of a locule enlarged to show a dividing cell of inner parietal layer which contributes to the tapetum and middle layer II. C, Anther lobe with amoeboid tapetum enveloping the microspore tetrads. D, Anther lobe showing numerous microspore mother cells, surrounding them during meiosis is the detached tapetum. E, Late anaphase of division I. F, After telophase I, note beginning of transverse furrow. G, Simultaneous division of microspore. H, Nonsynchronous division of microspores in a tetrad. I, One pollen grain out of a tetrad germinating. (A, B, D, *Drimys winteri*, after Bhandari & Venkataraman, 1968; C, I, *Pseudowintera colorata*, after Bhandari, 1963; E–G, *Zygogynum baillonii*, after Swamy, 1952; H, *Pseudowintera axillaris*, after Sampson, 1963.)

in permanent tetrads at the 2-celled stage (FIGURE 2 I). In *Zygogynum* (Swamy, 1952) all the pollen grains germinate, while in *Pseudowintera colorata* only one germinates on the stigma; the rest degenerate (FIGURE 2 I).

The ovules are laminar, anatropous, bitegmic, and crassinucellate; the micropyle is formed by the inner integument alone (FIGURE 3 A). A

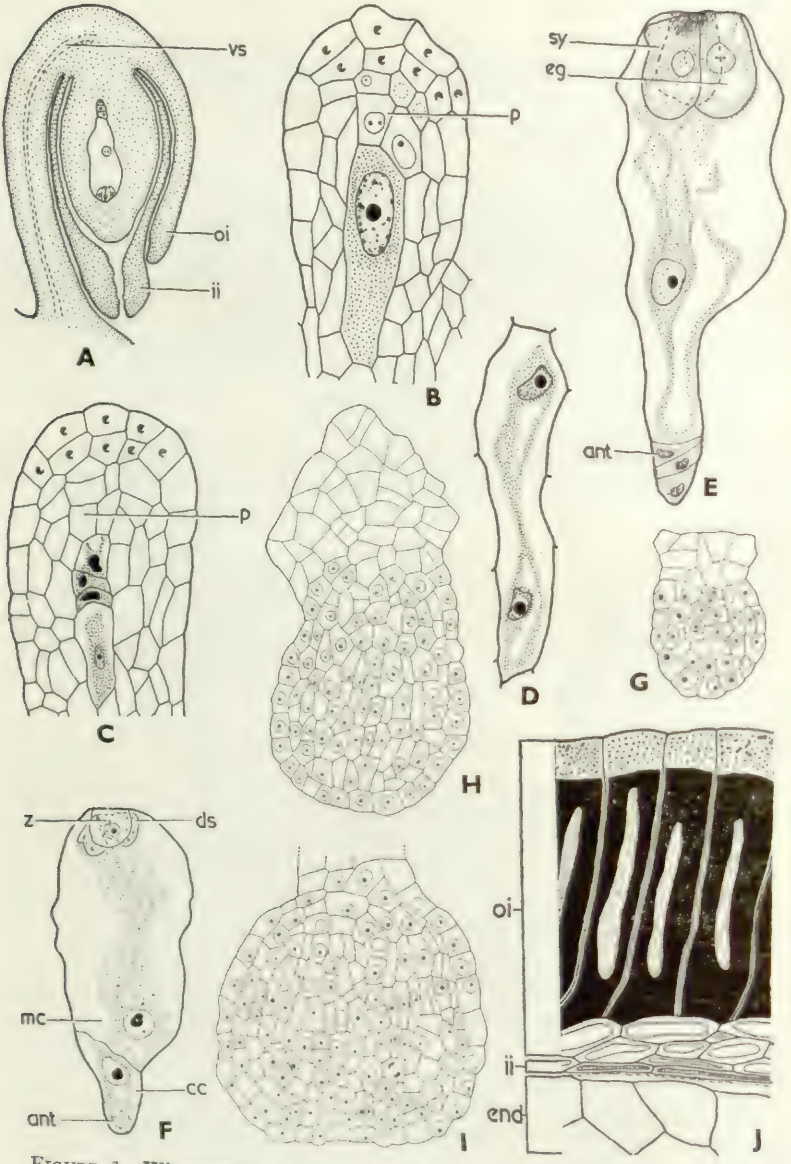

FIGURE 3. **Winteraceae.** (*ant*, antipodal cells; *cc*, chalazal chamber; *ds*, degenerating synergid; *e*, epidermal cell; *eg*, egg; *end*, endosperm; *ii*, inner integument; *mc*, micropylar chamber; *oi*, outer integument; *p*, parietal cell; *sy*, synergid; *vs*, vascular supply; *z*, zygote.) A, Longitudinal section of ovule at mature embryo sac stage. B, Longitudinal section of nucellus showing two-layered parietal tissue and megaspore mother cell. C, Linear tetrad with chalazal megaspore functioning. D, Two-nucleate embryo sac. E, Mature embryo sac, note basal vacuole in the egg also. F, Two-celled endosperm with micropylar and chalazal chambers. G–I, Stages in development of embryo;

single hypodermal archesporial cell divides periclinally to cut off a parietal cell which forms a massive parietal tissue (FIGURE 3 B); the nucellar epidermis may also contribute to the parietal tissue (FIGURES 3 B, C). A linear or T-shaped tetrad is produced at the end of reduction divisions in the megaspore mother cell (FIGURE 3 C). The chalazal megaspore functions to form the Polygonum type of embryo sac (FIGURES 3 C–E). In *Pseudowintera* the synergids have filiform apparatus; the polar nuclei fuse before fertilization and the three small uninucleate antipodal cells are ephemeral (FIGURE 3 E).

Triple fusion precedes syngamy and the endosperm is *ab initio* cellular. In *Pseudowintera* the first division may be transverse (FIGURE 3 F) or vertical. Both the chambers contribute towards the formation of endosperm tissue. The embryogeny has been worked out only in *Drimys* (Bhandari & Venkataraman, 1968) and it is irregular (FIGURES 3 G–I), not conforming to any particular type of Johansen (1950). A suspensor is present but the embryo perhaps remains undifferentiated at the time of shedding of the seeds (FIGURES 3 H, I).

The seed coat is formed chiefly by the outer integument, and the inner becomes almost crushed and is represented by a thin strip of greatly stretched cells (FIGURE 3 J). The cells of the epidermis of the outer integument become elongated, thick walled, brittle, and extremely hard.

The pericarp is about 14–16-layered and remains fleshy and parenchymatous. In *Pseudowintera* meristematic plates of tissue develop in between the maturing seeds so that the fruit becomes chambered. Numerous ethereal oil cells, tannin cells, and stone cells are interspersed in the tissue of the fruit-wall. The pericarp is differentiated into outer tough and coriaceous, and inner spongy, soft regions. The inner region develops numerous ingrowths between the seeds.

Only two genera, *Drimys* and *Pseudowintera* (*see* Borgamann, 1964; Darlington & Wylie, 1955; Hotchkiss, 1955; Raven & Kyhos, 1965), are known cytologically. In *Drimys* (section TASMANIA) $n = 13$ or 14 has been reported in literature. However, Raven and Kyhos (1965) have shown that reports of $2n = 28$ are erroneous since this number is expressed because of a precocious disjunction in one of the bivalents making the configuration as $n = 12_{II} + 2_{I}$. Similarly, the court $n = 38$, for *D. winteri* (Whitaker, 1933) has been shown to be erroneous and as reinvestigated by Raven and Kyhos (1965) it is $n = 43$. *Drimys lanceolata* occurs in two cytological races, the diploid with $2n = 26$, and the triploid having $2n = 39$; *Pseudowintera colorata* also shows $n = 43$.

Degeneriaceae. The Degeneriaceae are monotypic and endemic to the Fiji Islands. The family has a number of primitive features such as the

I, undifferentiated heart-shaped embryo contained in a seed obtained from mature fruit. J, Part of seed coat to show crushed and depleted cells of outer and inner integuments; epidermis of radially elongated outer integument constitutes major part of seed coat. (A–F, J, *Pseudowintera colorata*, after Bhandari, 1963; G–I, *Drimys winteri*, after Bhandari & Venkataraman, 1968.)

broad laminar stamens (without any differentiation into filament, connective, and anther) having four microsporangia embedded on the abaxial surface; conduplicate carpel devoid of any style and stigma, and instead, having a decurrent stigmatic crest; laminar ovules; multilacunar node; and a primitive type of wood.

Swamy (1949) has worked out the embryology, and Dahl and Rowley (1965) the ultrastructure of pollen of *Degeneria vitiensis*. In a young anther four groups of archesporium differentiate (FIGURE 4 A). The wall of the anther on the abaxial surface comprises an epidermis, 1-layered fibrous endothecium, three or four middle layers, and a single-layered tapetum with binucleate cells (FIGURES 4 B, C). At the time of dehiscence only the epidermis and endothecium persist; towards the connective region some more layers develop thickenings like that of the endothecium. The cytokinesis is simultaneous and results in tetragonal tetrads (FIGURE 4 D). The germinal furrow begins to develop on the distal end even when the microspores are in tetrads (FIGURES 4 D, F). The generative cell is cut off towards the distal end (FIGURE 4 E). The pollen grains are monocolpate and 2-celled at the shedding stage.

There are nearly 30 to 32 ovules in a carpel. They are laminar, anatropous, bitegmic and crassinucellate. The micropyle is formed by the inner integument alone (FIGURE 4 I); a funicular obturator is very conspicuous and is comprised of elongated and densely cytoplasmic cells of the epidermis. The 1-celled archesporium is hypodermal and a massive tissue is formed by the primary parietal cell (FIGURE 4 H). A linear tetrad is produced, of which the chalazal megaspore (FIGURE 4 I) functions to form the Polygonum type of embryo sac (FIGURE 4 J). The synergids and the antipodal cells are short-lived.

After pollination, when the pollen grains fall on the stigmatic surface, they germinate and the pollen tube is put forth from one of the two broader ends of the germinal furrow (FIGURE 4 G). Triple fusion precedes syngamy and the endosperm is *ab initio* cellular (FIGURE 4 K). The mature endosperm is ruminate (FIGURE 4 T). The zygote divides only after a massive endosperm tissue is formed (FIGURE 4 L). Although the first division of the zygote is transverse; subsequent segmentation does not follow any strict pattern (FIGURES 4 M–Q). However, the process of tissue differentiation later becomes quite stabilized. The mature embryo is either tri- or tetracotyledonous having a short suspensor, a bulbous hypocotyl, and well differentiated cotyledons (FIGURES 4 R, S).

The seed coat is formed by the outer vascularized integument whereas the inner integument becomes reduced to a membranous layer of crushed cells. The testa is differentiated into an outer succulent region with numerous groups of oil cells and an inner ridged stony region enclosing the ruminate endosperm (FIGURES 4 T, U).

Recently Raven and Kyhos (1965) reported $n = 12$ for the monotypic family and that, therefore, constitutes the basic haploid number. The karyotype has not been investigated.

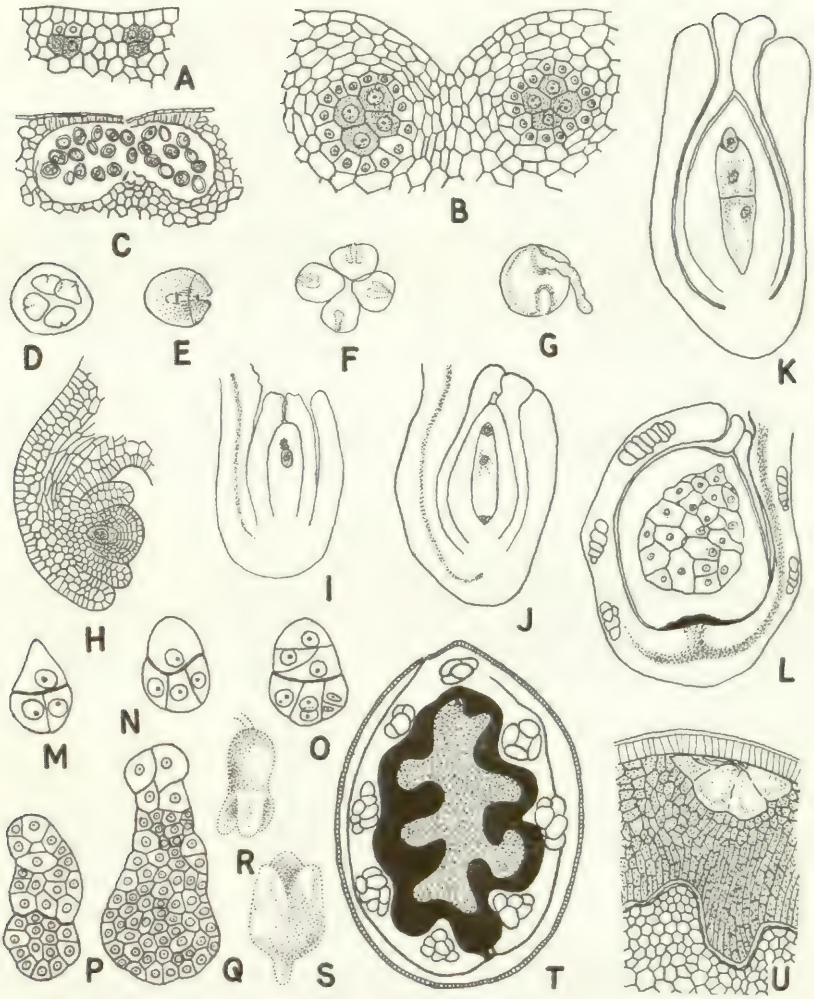

FIGURE 4. **Degeneriaceae.** A, Part of transverse section of anther showing two groups of archesporium. B, Same, showing differentiation of wall layers. C, Two adjacent microsporangia after dehiscence showing two-celled pollen grains. D, Tetragonal tetrad of spores. E, Microspore showing formation of the generative cell. F, Tetrad showing development of colpi in microspores. G, Germinating pollen grains. H, Longitudinal section of ovule showing megaspore mother cell and parietal tissue. I, Same, showing linear tetrad of which chalazal megaspore is functional. J, Same, showing mature embryo sac. K, Two-celled endosperm. L, Longitudinal section of developing seed, showing massive endosperm and zygote. M–Q, Stages in development of embryo. R, S, Tricotyledonous embryos showing suspensor, hypocotyl, and cotyledons. T, Longitudinal section of mature seed showing outer fleshy and inner stony regions, ruminate endosperm, and small embryo. U, Part of seed coat enlarged from FIGURE T. (A–T, *Degeneria vitiensis*, after Swamy, 1949.)

Annonaceae. The Annonaceae is the largest of all the woody magnolian families and comprises 120 genera with approximately 2,100 species. The family is cosmopolitan and well represented in tropical and subtropical to temperate regions of the world.

Only one tenth of the total number of genera and about 15 species have been worked out embryologically. In a young anther the archesporium is either multicelled as in *Artabotrys* (Asana & Adatia, 1947) and *Miliusa* (Periasamy & Swamy, 1959), or it is differentiated as a uniseriate row (FIGURE 5 A) in *Annona* (Juliano, 1935), *Cananga* (Periasamy & Swamy, 1959), *Asimina* (Locke, 1936), *Monodora* and *Xylopia* (Lecomte, 1896). In the latter group of plants some of these cells form sterile septae (FIGURE 5 D) so that individual microspore mother cells or a group of them become separated (Juliano, 1935; Periasamy & Swamy, 1959). The tapetum along the protruding part of the microsporangium is parietal in origin (FIGURES 5 B, C). The anther wall is constituted of the epidermis, the fibrous endothecium, and three or four middle layers (FIGURE 5 F). The tapetum is glandular as in *Artabotrys*, *Cananga*, and *Miliusa* or amoeboid as in *Annona* (Juliano, 1935; Asana & Adatia, 1947), *Polyalthia*, *Unona*, and *Cananga* (*see* Asana & Adatia, 1947). Cells of the tapetum are binucleate or tetranucleate, or the four nuclei fuse to form a tetraploid nucleus (FIGURE 5 E). In *Cananga odorata* (Periasamy & Swamy, 1959), *Asimina* (Herms, 1907), and *Annona* (Juliano, 1935) the tissue of the sterile septae in the microsporangium behave as the tapetum (FIGURE 5 D) and therefore, it may be regarded that tapetum is being contributed by the parietal as well as the sporogenous tissues. In the light of Periasamy and Swamy's (1959) observations on *Cananga* and *Miliusa*, the genera reported to have amoeboid tapetum need a reinvestigation.

The process of cytokinesis is successive in *Annona* (Juliano, 1935; Sastri, 1957) and *Uvaria* (Sastri, 1957) but simultaneous in *Cananga* (Periasamy & Swamy, 1959), *Annona* (Samuelson, 1914), *Asimina* (Locke, 1936), *Polyalthia*, and *Saccopetalum* (Sastri, 1957). In *Cananga* and *Miliusa* the first furrow starts at the end of heterotypic division but is completed along with the second at the termination of homotypic division (FIGURES 5 G, H). The microspore tetrads are tetrahedral, tetragonal, or decussate. In *Annona* the pollen grains remain in permanent tetrads. At the time of shedding the pollen grains are 2-celled (FIGURE 5 J), the generative cell being cut off towards the distal end (FIGURE 5 I); they are monocolpate or acolpate (rarely with a slit-like aperture as in Magnoliaceae); and the exine is psilate, verrucate, reticulate, or even echinulate (*see* Erdtman, 1952).

The ovules are anatropous, bitegmic, tritegmic (FIGURE 6 B) and crassinucellate. The micropyle, however, is formed by the outer or inner integument or by both, the middle remains rather arrested (FIGURE 6 B). The outer integument is vascularized as in some Magnoliaceae. In *Cananga odorata* (Periasamy & Swamy, 1956) and *Saccopetalum tomentosum* (Sastri, 1957) the carpel is conduplicate and the ovules receive their vasculari-

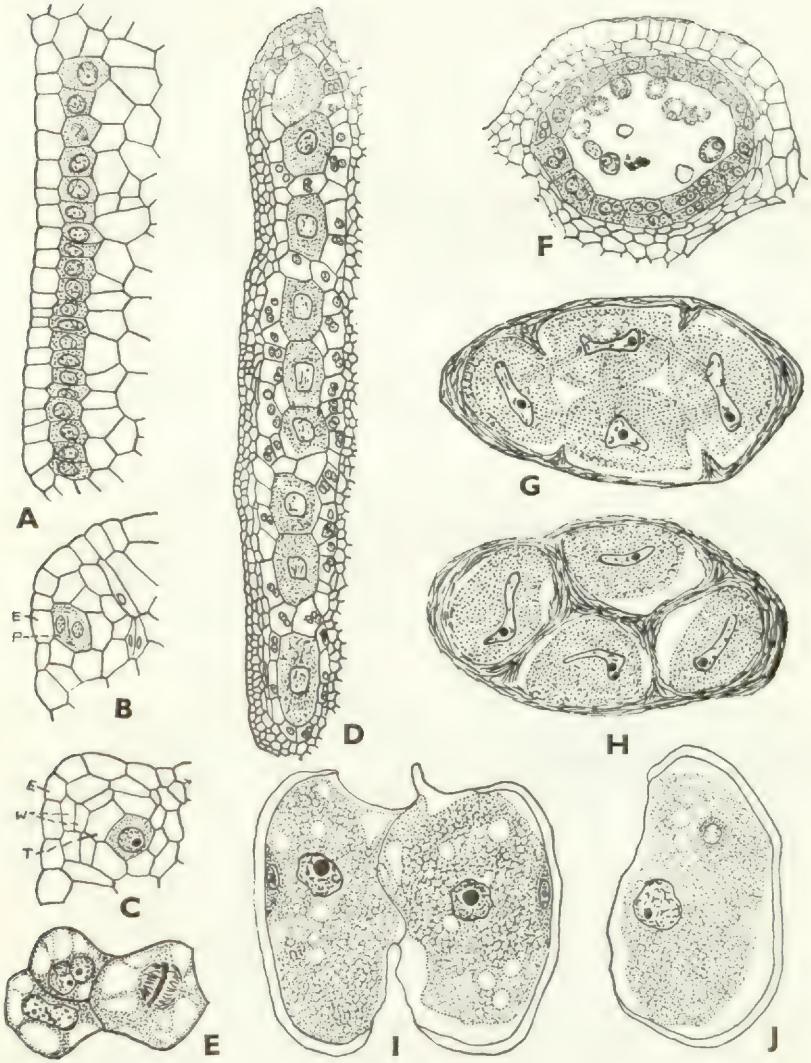

FIGURE 5. **Annonaceae.** (*e*, epidermis; *p*, parietal layer; *t*, tapetum; *w*, wall layers.) A, Longitudinal section of a young anther locule showing uniseriate row of archesporial cells. B, C, Transections of stamens showing successive stages in development of wall layers. D, Longitudinal section of anther locule showing sterilization of sporogenous cells and formation of sterile septa. E, Behavior of nuclei of tapetal cells. F, Transection of anther showing wall layers, tapetum and microspores. G, H, Stages in cytokinesis by furrowing. I, Two-celled pollen grains soon after division of microspore nucleus. J, Two-celled pollen; generative cell with granular cytoplasm surrounded by hyaline membrane. (A–J, *Cananga odorata*, after Periasamy & Swamy, 1959.)

zation by the traces from the dorsal bundles. A hypostase has been reported in *Asimina* and *Artabotrys*. An aril is present in some members (Corner, 1948). The hypodermal archesporium is 1- to few-celled (FIGURE 6 A), and the massive parietal tissue is formed by the primary parietal cell (FIGURE 6 B). At the end of meiosis I a dyad is formed (FIGURE 6 B) which results in a linear tetrad, of which the chalazal megaspore functions (FIGURE 6 C). The development of the female gametophyte conforms to the Polygonum type. The synergids are hooked and the antipodal cells remain uninucleate (FIGURE 6 D). The synergids and 3 small antipodal cells degenerate immediately after fertilization.

The endosperm is cellular. The first and the following few divisions in the endosperm are transverse so that a uniseriate row of endosperm cells is formed (FIGURE 6 E, F). Later the endosperm becomes massive and ruminate (FIGURE 6 K). The zygote divides transversely (FIGURE 6 G), followed by vertical division in the resulting two cells. In *Polyalthia longifolia* (Sastri, 1955a) the derivatives of the basal cell give rise to hypophysis and suspensor, whereas the derivatives of the terminal cell form two piers, upper *pc* forming the central cylinder of stem and cotyledons, and lower *pc* contributing entirely to the hypocotyledonary regions. In *Cananga odorata* (Periasamy & Swamy, 1961), the basal cell undergoes a transverse division (FIGURES 6 H, I). The derivatives of the octants form a globular embryo (FIGURE 6 J) which differentiates later into a dicot embryo. The embryogeny, therefore, follows the Trifolium or Lotus variation of the Onagrad type.

The seed coat is formed chiefly by the outer integument alone, although the inner integument may persist in some genera (FIGURES 6 K, L). The ruminations, which are produced by the outer integument, are pushed into the developing endosperm (FIGURE 6 L). During this process the tissue of the nucellus and the inner integument become compressed and line the ingrowths of the outer integument. These ruminations are not vascularized. A poorly or a well-developed aril is present in the annonaceous seeds (FIGURE 6 K). The ripe seeds have copious endosperm with or without starch (Corner, 1948) and a small dicotyledonous embryo. Occasionally composite fruits (syncarps) are produced, as in *Annona*.

Out of 120 genera only 15 have been worked out cytologically (Darlington & Wylie, 1955; Mangenot & Mangenot, 1957, 1958; Mangenot *et al.*, 1957; Miège, 1954, 1960; Pawar *et al.*, 1956). Of these, 8 genera have x = 8, 3 have x = 9, and two have x = 7. *Rollinia orthopetala* shows $n = 24$ which according to Darlington and Wylie (1955) may be doubtful. Only *Artabotrys odoratissimus* has forms with $n = 8$ or 9, while *Asimina triloba* is found to be either diploid, with $2n = 18$, or triploid, $2n = 27$. Therefore, the family is characterized by three basic numbers, x = 7, 8, and 9. Since a larger number of genera and species possess x = 8, it is likely that the other genera evolved by addition or subtraction of one chromosome, or by a multiple of this base number.

Myristicaceae. The Myristicaceae include 15 genera and nearly 250 species which are met with in new world tropics, Africa, and Asia. Vas-

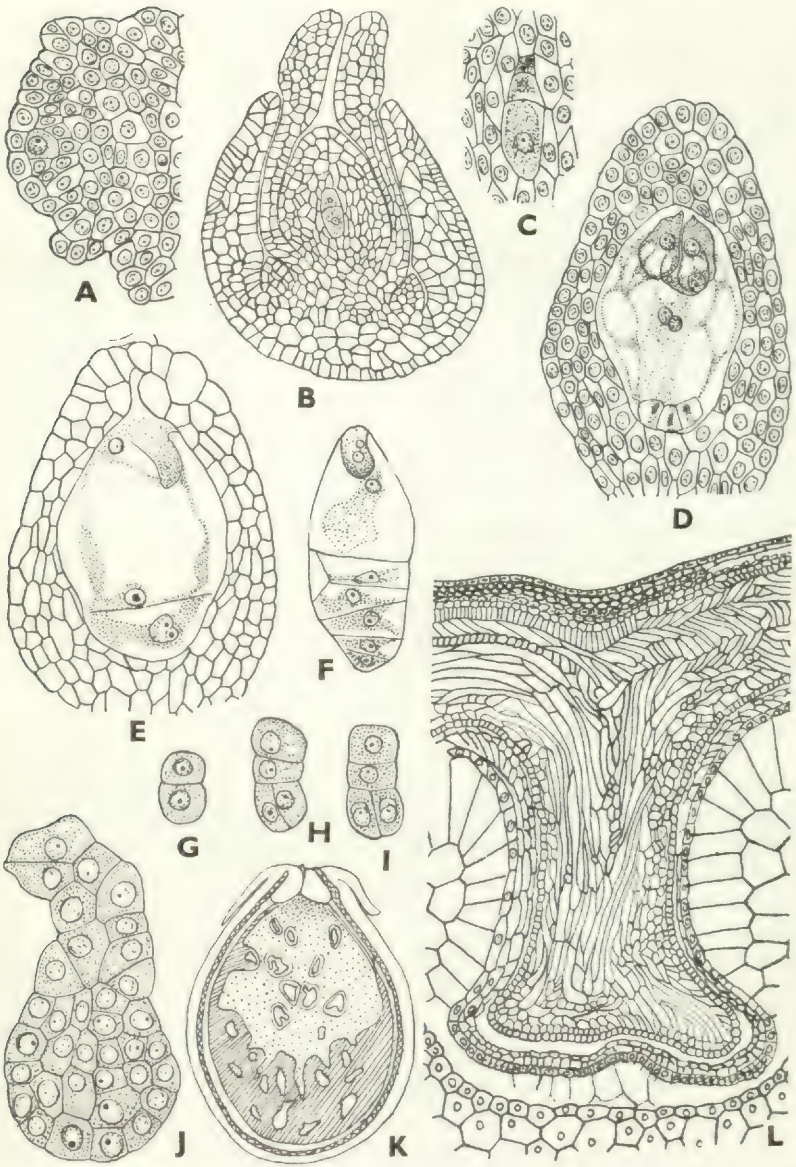

FIGURE 6. **Annonaceae.** A, Longitudinal section of ovule showing hypodermal archesporial cell and origin of integuments. B, Transmedian longitudinal section of the ovule just after the initiation of the middle integument. C, Linear tetrad, the three micropylar megaspores degenerating. D, Mature embryo sac. E, Longitudinal section of 2-celled endosperm and nucellus. F, Longitudinal section of young endosperm showing linear series of cells with a larger micropylar one. G–J, Stages in embryogenesis. K, Median longitudinal section of seed at the time when endosperm expands rapidly. L. Fully formed rumination process with nucellar remains and endosperm in immature seed. (A–L, *Cananga odorata*, after Periasamy & Swamy, 1961.)

cular anatomy of the flower, aril, and embryology of only *Myristica* spp. has been worked out (Camp & Hubbard, 1963; Joshi, 1946; Nair & Bahl, 1956; Nair & Pillai, 1959; Periasamy, 1961; Sastri, 1955b).

The anther wall is composed of epidermis, fibrous endothecium, two ephemeral middle layers, and a single-layered glandular tapetum comprising uninucleate cells. At the end of meiosis the successive type of cytokinesis in the microspore mother cells results in isobilateral tetrads. The pollen grains are 2-celled and 1-sulcate.

The anatropous ovules are bitegmic and crassinucellate; the micropyle is constituted by the inner integument. A single archesporial cell cuts off a parietal cell which by periclinal and anticlinal divisions forms a massive parietal tissue. The megaspore mother cell is deeply buried and forms a linear tetrad at the end of meiosis. The chalazal megaspore is functional which gives rise to the Polygonum type of embryo sac.

The endosperm is nuclear and later becomes cellular and ruminate. The embryo development has not been worked out. The seed coat is formed by the outer integument whereas the ruminations are developed from the massive tissue formed by the meristematic chalazal region (Periasamy, 1961). The aril which develops from the outer integument is vascularized and forms a network covering the mature seed.

Only *Myristica fragrans* (Simmonds, 1954) and *Pycnanthus angolensis* (Mangenot & Mangenot, 1957) have been worked out and these show $n = 21$ and $n = 19$, respectively. The basic number is doubtful and may turn out to be $x = 7$ but requires more intensive work before anything can be finally said.

Canellaceae. The family Canellaceae comprises six genera and 20 species distributed disjunctively from Venezuela to southern Florida, tropical America, Puerto Rico, Madagascar, and tropical Africa.

Parameswaran's (1961, 1962) is the only embryological account available for *Canella alba* and *Warburgia stuhlmannii*. The androecium of the family is syngenesious. The paired anther thecae arise in the form of longitudinal ridges i.e. protuberant columns of cells. At the outer corners of the column hypodermal archesporial cells become differentiated, then divide periclinally to form the primary parietal cell and the sporogenous cells (FIGURE 7 A). The primary parietal cell forms 5-layered tissue, of which the innermost forms the glandular tapetum, the next 2 or 3 layers are the middle layers, while the outer gives rise to the fibrous endothecium (FIGURE 7 B). The tapetal cells become bi- or tetranucleate after which the nuclei fuse to form a tetra- or octoploid nucleus. In *Canella alba* and *Warburgia stuhlmannii* the inner wall of the tapetum becomes studded with minute protuberances (Ubisch granules) along its inner and outer surfaces (FIGURE 7 E). In the dehisced anther the wall is comprised of only the persisting protuberant epidermis and fibrous endothecium; the rest of the layers degenerate (FIGURE 7 C). The microspore mother cells produce tetrahedral tetrads after meiosis (FIGURE 7 F). The generative cell is cut off towards the proximal pole even before the pollen grains are

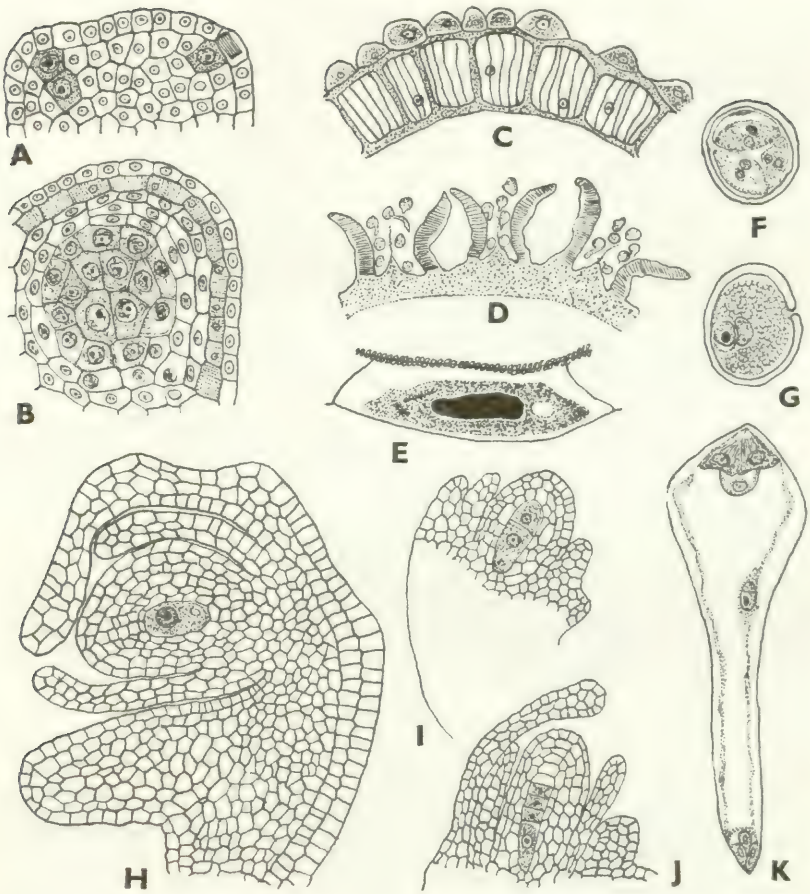

FIGURE 7. **Canellaceae.** A, Transection of sector of young anther primordium showing archesporial cell has divided into primary parietal and sporogenous cells. B, Same, showing epidermis, endothecium, three wall layers, tapetum, and group of microspore mother cells. C, Endothecium and persisting epidermis. D, Germinating pollen grain, lodged in dehisced anther thecae. E, Tapetal cell showing ubisch granules along both surfaces of tangential wall. F, Microspore tetrad after division of microspore nucleus into generative and vegetative cells. G, Sectional view of mature 2-celled pollen showing germinal furrow. H, Longitudinal section of young ovule containing megaspore mother cell. I, Dyad stage. J, Linear tetrad — note accelerated growth of outer integument at one side. K, Mature embryo sac. (A–G, K, *Canella alba*; H–J, *Warburgia stuhlmanii*, after Parameswaran, 1962.)

released from the tetrads (FIGURE 7 F). A large number of pollen grains germinate *in situ* (FIGURE 7 D), and in such germinated pollen the sperm and the elongated vegetative nucleus occupy the terminal part of the pollen tube. The pollen grains are monocolpate (FIGURE 7 G) and the col-

pus develops along the distal pole concurrently with division of the microspore nucleus.

The ovules are hemianatropous, bitegmic and crassinucellate (FIGURE 7 H). The two integuments differentiate simultaneously but the outer grows faster and asymmetrically on the antiraphe side (FIGURE 7 H, J). The micropyle is zigzag and is constituted by both the integuments. The hypodermal archesporium is 1-celled. The primary parietal cell forms a massive parietal tissue (FIGURE 7 H) so that the female gametophyte lies deeply buried in the nucellus. In *Warburgia* a linear tetrad of megaspores is formed, of which the chalazal functions (FIGURES 7 I, J) to form the Polygonum type of female gametophyte. The synergids have a conspicuous filiform apparatus, the polar nuclei fuse before fertilization and 3 uninucleate antipodal cells are organized (FIGURE 7 K). Both the antipodals and the synergids are ephemeral.

The development of endosperm has not been worked out; however, Parameswaran (1961) has recorded ruminate endosperm in *Cinnamosma*. The ruminations formed by the seed coat are nonvascularized. The embryogeny is unknown but the mature seed contains a slightly curved embryo embedded in a copious oily endosperm tissue.

The inner and outer epidermis of the inner and outer integuments respectively, constitute the seed coat. The epidermal cells of the outer integument are infiltrated with some black contents, and become sclerotic.

The family has $n = 11$ or 13, and these may also be the basic numbers.

Illiciaceae. Illiciaceae is a monogeneric family comprising nearly 42 species which are met with in China, Japan, Indochina, West Indies, Sikkim, and India.

Hayashi (1960, 1963) has investigated the embryology of *Illicium floridanum* and *I. anisatum*. The anther wall constitutes the epidermis, the endothecium which develops fibrous thickenings after the pollen grains have been formed, 2 or 3 middle layers, and the irregularly 2-layered glandular tapetum. The cells of the tapetum are considered to have originated from the sporogenous tissue surrounding the microspore mother cells. Critical stages to justify the sporogenous origin of the tapetum are, however, wanting. At the end of meiosis II, simultaneous cytokinesis results in tetrahedral tetrads. The pollen grains are isopolar, tricolporate and 2-celled at the time of shedding.

The ovules are anatropous, bitegmic, and crassinucellate. The female archesporium is single-celled. The parietal cell divides anticlinally as well as periclinally and forms a massive parietal tissue resulting in a deeply buried megaspore mother cell. The chalazal megaspore of a linear tetrad gives rise to a Polygonum type of female gametophyte. The three uninucleate antipodal cells are ephemeral.

The development of endosperm is *ab initio* cellular (Hayashi, 1963). Earle's (1938) report of nuclear endosperm seems to be erroneous. The development of the embryo conforms to the Asterad type. Recently Stone and Freeman (1968) have worked out the cytotaxonomy of two species of *Illicium*, *I. floridanum* and *I. parviflorum* and found that the former

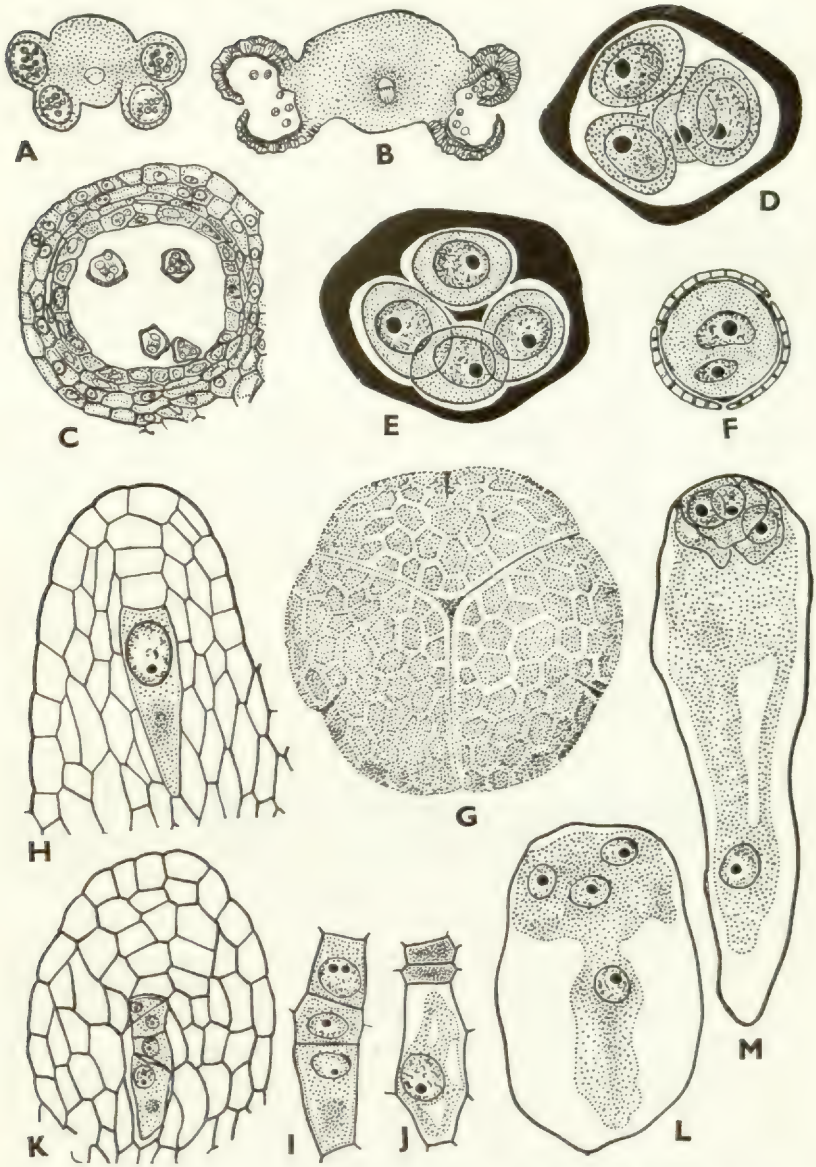

FIGURE 8. **Schisandraceae.** A, B, Transections of anther at the microspore and 2-celled stage of pollen grain; in B note irregularly 1- or 2-layered fibrous endothecium. C, Anther locule to show wall layers. D, E, Tetrahedral and decussate microspore tetrads. F, Two-celled pollen grain. G, Pollen grain with a triradiate mark formed by meeting of three furrows; exine is reticulate. H, Longitudinal section of nucellus showing parietal cells and megaspore mother cell. I, Triad. J, Functioning megaspore, degenerated upper dyad cell, and middle non-functioning megaspore. K, A tetrad of megaspores. L, Four-nucleate embryo sac. M, Mature female gametophyte. (A–J, L, M, *Schisandra grandiflora*, after Kapil & Jalan, 1964; K, *S. chinensis*, after Swamy, 1964.)

has $n = 13$ whereas the latter possesses $n = 14$. They suggest that Whitaker's (1933) report of *I. floridanum* and *I. anisatum* (*I. religiosum*) as having $n = 14$ is, perhaps, incorrect. They explain the origin of $n = 13$ in *I. floridanum* by aneuploidy from $n = 14$ of *I. parviflorum*.

Schisandraceae. Two genera of woody vines, *Schisandra* and *Kadsura*, comprise the family Schisandraceae which is distributed in eastern and southeastern Asia and Malesia. Only *Schisandra glabra* is a native of America. In India there are four species found in the eastern and western Himalayas. In the Schisandraceae amongst many characters, the formation of a modified column by the basal connation of the filaments of the stamens, the conduplicate carpel with ventral stigmatic crest, and its distal extension to form a non-vascularized pseudostyle are of interest.

The anther wall comprises a persistent epidermis, 1- or 2-layered fibrous endothecium, 2 or 3 middle layers, and irregularly bilayered glandular tapetum (FIGURES 8 A–C). As the anther matures the epidermal cells become papillate and several of these become packed with tannin. The endothecium develops vertically oriented fibrous thickenings whereas the middle layers degenerate soon after the reduction divisions are completed. The cells of the tapetum become multinucleate, and the nuclei fuse to form polyploid masses. At the time of dehiscence, the epidermis, endothecium, and remnants of the middle layers persist (FIGURE 8 B). Numerous ethereal oil cells are present in the connective tissue. The cytokinesis is simultaneous, resulting in tetrahedral and decussate tetrads (FIGURES 8 D, E). The pollen grains are tri- or hexacolpate (FIGURE 8 G). The latter have three small and three large meridionally arranged furrows. The large colpi fuse at one end to form a triradiate mark (FIGURE 8 G). The pollen grains are shed at the 2-celled stage (FIGURE 8 F).

The ovules are anatropous, bitegmic, and crassinucellate. Both the integuments organize the micropyle. A single hypodermal cell cuts off a primary parietal cell which divides periclinally to produce 3 or 4 parietal cells (FIGURE 8 H). In *Schisandra grandiflora* (Kapil & Jalan, 1964) after a dyad is formed, the lower dyad cell divides to give rise to a triad (FIGURE 8 I). The chalazal megaspore functions (FIGURE 8 J) to produce the Polygonum type of embryo sac (FIGURES 8 L, M). The antipodal cells are ephemeral and degenerate soon after their inception (FIGURE 8 M). Yoshida (1962) also reported the Polygonum type of embryo sac in *S. chinensis*. In *S. chinensis*, however, Swamy (1964) reported monosporic as well as bisporic development of the embryo sac (FIGURES 8 K; 9 A, B), and according to him the organization of the mature embryo sac is accomplished after the 4-nucleate stage (Oenothera type). The antipodal cells and one of the polar nuclei are lacking. So far no bisporic embryo sac with such an organization has been recorded. Keeping in view the divergent interpretation concerning the development of the female gametophyte, a reinvestigation is much desired.

The pollen grains are monosiphonous, fertilization is porogamous and one or both the synergids become crushed during this process. The endo-

sperm is cellular. The first division is transverse and results in a large micropylar and a small chalazal chamber (FIGURE 9 C). Further growth in both the chambers results in a massive endosperm tissue which fills almost the entire cavity of a mature seed (FIGURES 9 D, E). The division of the zygote is either transverse or vertical (FIGURES 9 F, G). The derivatives of *ca* form the octant having 4 cells in tier 1′ and 1 (FIGURES 9 H–J). Embryogeny follows the Asterad or Onagrad type. The mature embryo is dicotyledonous (FIGURE 9 E).

The seed coat is contributed by both the integuments, the outer integument comprising an epidermis of macrosclereids, 2 or 3 subepidermal layers of brachysclereids, followed by 2 or 3 layers of parenchymatous tissue; whereas the inner integument persists as a thin 2-layered tissue of thick-walled cells (FIGURE 9 K). The fruit wall is fleshy and succulent and comprises 14 to 16 layers of enlarged parenchymatous cells. There are numerous ethereal oil cells interspersed in the outer epidermis of the pericarp.

The two genera, *Schisandra* and *Kadsura*, of the family Schisandraceae possess $n = 14$ (Darlington & Wylie, 1955; Stone, 1968). The basic number was thought by Darlington and Wylie (1955) to be $x = 7$. According to Stone (1968) the karyotype is different from that of Illiciaceae in being nearly symmetrical and showing an absence of subterminal chromosomes.

Monimiaceae. In the Monimiaceae there are about 34 genera and 450 species met with in tropical and subtropical regions with distributional centers in Australia, Polynesia, Madagascar, tropical Africa, South America, and Mexico.

Of the larger number of genera and species, the embryology of only *Peumus boldus* (Mauritzon, 1935) has been worked out in detail, in addition to some fragmentary information that exists on *Siparuna eggersii* (Heilborn, 1931) and *Mollinedia* (Peter, 1920). The anther wall comprises epidermis, fibrous endothecium, 2 or 3 middle layers, and a 1-layered glandular (periplasmodial in *Atherosperma*, *see* Sastri, 1963) tapetum. At the end of meiosis, tetrahedral tetrads of microspores are formed by simultaneous cytokinesis. The pollen grains are shed individually or they remain in permanent tetrads in *Hedycarya angustifolia* (Money, Bailey, & Swamy, 1950). They are mono-, bi-, or acolpate and are shed at the two-celled stage.

The ovules are anatropous unitegmic (*Siparuna*) or bitegmic (*Peumus boldus*) and crassinucellate. The micropyle in *Peumus* is formed by both the integuments. The nucellar epidermis at the tip undergoes periclinal divisions (FIGURE 10 F) so that a 4–6-layered nucellar cap is formed. At the mature embryo sac stage a conspicuous hypostase is present. The female archesporium is multicelled in *Siparuna* but is one-celled in *Peumus* (FIGURES 10 A, F). The archesporial cell forms the primary parietal cell which divides repeatedly to result in a massive parietal tissue so that the megaspore mother cell is deeply buried in the nucellus (FIGURES 10 A, F).

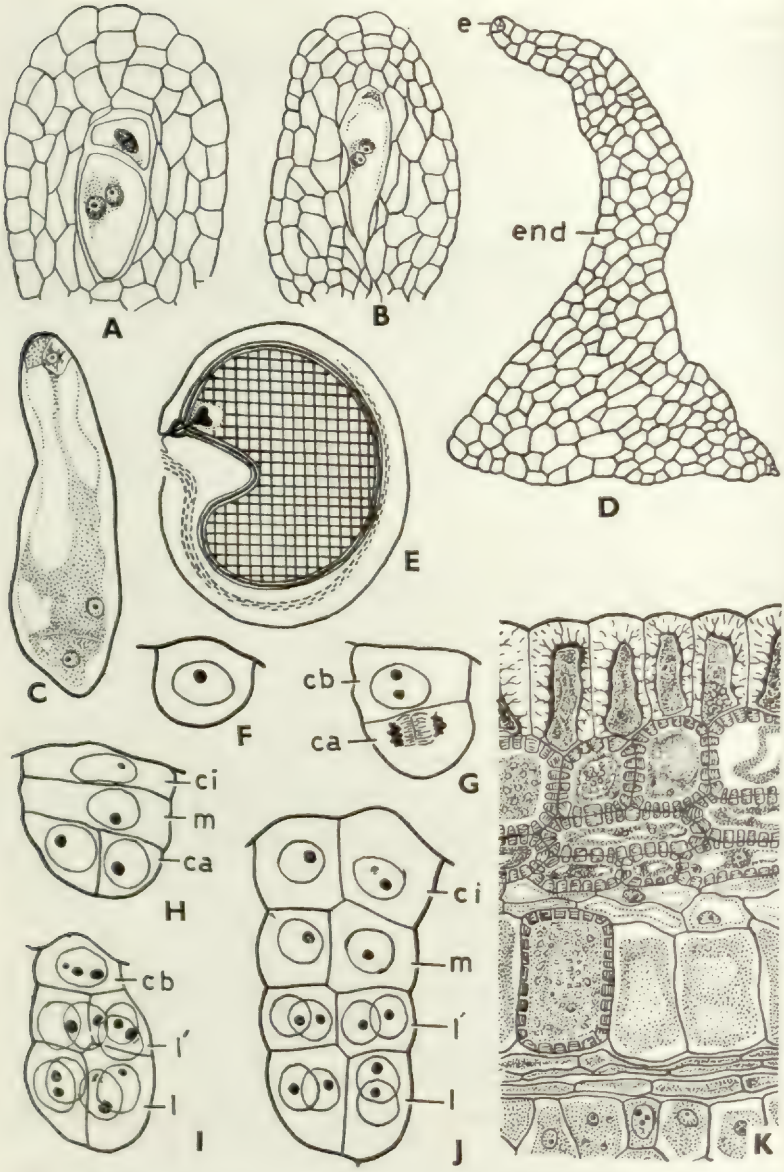

FIGURE 9. **Schisandraceae.** (*e*, embryo; *end*, endosperm.) A, Chalazal dyad cell with two megaspore nuclei and micropylar dyad cell in meiosis II. B, Micropylar dyad cell degenerating and chalazal cell with two megaspore nuclei. C, Two-celled endosperm. D, Endosperm at 4-celled stage of embryo. E, Longisection of seed at dicotyledonous stage of embryo. F–J, Stages in development of embryo. K, Part of seed coat showing macrosclereids, brachysclereids, and other layers of testa. (A, B, *Schisandra chinensis*, after Swamy, 1964; C–K, *S. grandiflora*, after Kapil & Jalan, 1964.)

After meiotic division in the megaspore mother cell a linear tetrad is formed in *Siparuna* and *Mollinedia* (FIGURE 10 A). In *Siparuna* the chalazal megaspore functions and forms a long, tortuous chalazal tube with a vesicular tip (FIGURES 10 A, B). The tip of this tube bursts into another cell and discharges its contents (FIGURE 10 C). It forms a 4- or 5-nucleate female gametophyte that remains unorganized in *Siparuna*. However, in *Mollinedia* a normal embryo sac is formed. On the other hand, in *Peumus*, cytokinesis is suppressed after meiosis II, and subsequently the upper of the two dyad cells degenerates (FIGURE 10 G), whereas the lower functions to form the embryo sac (FIGURE 10 H). The development of the embryo sac is, therefore, of the Polygonum and Allium types. An antipodal complex of 5 to 20 cells is observed in *P. boldus* (FIGURE 10 I, J).

The development of endosperm is cellular. The first division is transverse which divides the embryo sac into a large micropylar and a much smaller chalazal chamber. The next division in the chalazal chamber is vertical and is followed by a few transverse divisions in the micropylar chamber (FIGURE 10 R). By repeated divisions both the chalazal and micropylar chambers form a massive endosperm tissue (FIGURE 10 S).

The zygote divides transversely (FIGURE 10 K) to form the cells *ca* and *cb*. Subsequently these two cells undergo either transverse or vertical division (FIGURES 10 L, M) or the cell *ca* may divide transversely whereas the cell *cb* divides vertically (FIGURE 10 N), indicating that there is a lot of plasticity in the pattern of divisions during early embryogeny. Later however, the derivatives of the *ca* form the embryo proper while those of the *cb* form a short suspensor (FIGURE 10 Q, R). In the mature seed there is a small embryo embedded in a copious endosperm. According to Johanson (1950), the embryogeny conforms to the Asterad type.

It must be realized that the foregoing embryological account is based on the information available for only two members out of a large number of taxa. Rather much variation can be expected in the embryological features matching well with the extensive diversification in vegetative and reproductive organs of taxa included in this family.

Chromosome counts of only two members, *Laurelia novaezelandiae* and *Kibara* sp. (Borgmann, 1964) have been made. Both genera show $n = 22$ but no karyotypic studies are available.

Calycanthaceae. The Calycanthaceae comprise two genera and about nine species distributed in the southeastern United States, Australia, China, and Japan.

The embryological literature has been summarized by Schnarf (1931). Recently Mathur (1969) has studied the development of male and female gametophytes in *Calycanthus*. The anther wall comprises the epidermis, fibrous endothecium, and glandular or periplasmodial tapetum. Meiosis in the microspore mother cell is abnormal. Cytokinesis is simultaneous resulting in tetrahedral or isobilateral tetrads. The mature pollen grains are 2-celled, rarely in tetrads in *Chimonanthus fragrans*, sterile and 2-nucleate. The exine is reticulate.

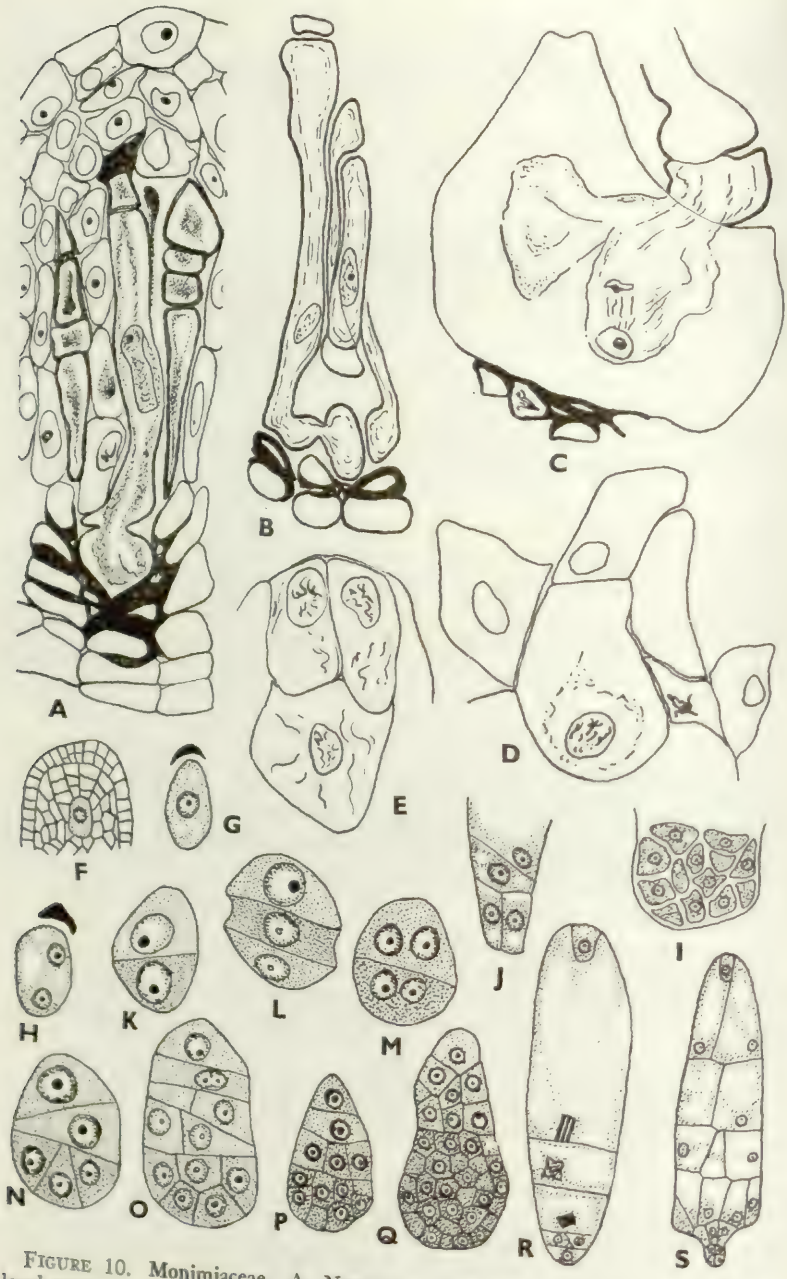

FIGURE 10. **Monimiaceae.** A, Nucellus with three megaspore tetrads; chalazal megaspore of central tetrad has grown out into an embryo-sac tube, ending in a chalazal vesicle immediately above the hypostase. B, Tubes from several tetrads, one from a micropylar megaspore — note nuclei still in tubes. C, Embryo sac plasma in nucellar cavity, still attached to mouth of embryo

The ovules are anatropous, bitegmic, and crassinucellate; the micropyle is formed by the inner integument alone. The cells of the nucellar epidermis divide periclinally to form a massive nucellar cap. The female archesporium is multicelled but parietal tissue is absent. Numerous megaspore mother cells function to form the linear tetrads, of which the chalazal megaspore functions to give rise to the Polygonum type of female gametophyte. Multiple embryo sacs are common. In the mature embryo sac the egg apparatus, one polar nucleus and the antipodal nuclei degenerate; syngamy and triple fusion therefore do not occur.

The development of the endosperm is autonomous and is *ab initio* cellular. Only nucellar embryos develop and polyembryony is frequent in *Calycanthus occidentalis*.

The two genera, *Calycanthus* and *Chimonanthus*, possess $n = 11$. The karyotype has not been investigated.

Lauraceae. The Lauraceae comprise about 31 genera and 2,250 species which are distributed in the tropics and warm-temperate areas of both hemispheres, especially Central and South America and southern Asia.

Of these, the embryology has been investigated only in *Cassytha* (Sastri, 1956, 1962), *Cinnamomum* (Chowdhury & Mitra, 1953; Giuliani, 1925; Sastri, 1958), *Laurus* (Battaglia, 1947; Mezzetti-Bambacioni, 1935, 1938, 1941), *Litsea* (Sastri, 1958), *Persea* (Schroeder, 1942, 1952), *Sassafras* (Coy, 1928), and *Umbellularia* (Mezzetti-Bambacioni, 1941).

The archesporium is multicelled and the wall layers are formed by the primary parietal layer (FIGURE 11 A). The anther wall comprises the persistent epidermis, fibrous or thick-walled endothecium, 2 middle layers, and amoeboid (*Cinnamomum*, *Laurus*, *Litsea*, *Persea*, *Sassafras*, *Umbellularia*) or glandular (*Cassytha*) tapetum (FIGURES 11 B–D). The tapetum is of parietal origin and its cells are bi-, tetra-, or multinucleate (FIGURES 11 B, C). Successive cytokinesis results in tetrahedral, isobilateral, T-shaped, or linear tetrads (FIGURES 11 E–G). The pollen grains are 2-celled, monocolpate or acolpate (*Cassytha*, *Laurus*). The exine is minutely spinescent.

The ovules are anatropous, bitegmic and crassinucellate. The micropyle is formed by both the integuments (FIGURE 12 B); in *Cassytha* (Sastri, 1962), however, the integuments do not grow beyond the nucellus so that the micropyle is broad and the overarching funiculus is in direct contact with the nucellus (FIGURE 11 K). The female archesporium is 1-celled (*Laurus*, *Umbellularia*) or multicelled as in *Cassytha* and *Cinnamomum* (FIGURES 11 H, J; 12 A). A massive parietal tissue is formed either from the parietal cell alone or by it and the nucellar epidermis

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sac tube. D, Sporophytic buds in micropylar part of nucellar cavity, the bud is just appearing. E, Bud at 3-celled stage. F, Longitudinal section of nucellus with megaspore mother cell. G, H, One- and two-nucleate embryo sac, upper dyad cell degenerating. K–Q, Stages in embryogenesis. R, S, Stages in development of endosperm. (A–E, *Siparuna eggersii*, after Heilborn, 1931; F–S, *Peumus boldus*, after Mauritzon, 1935.)

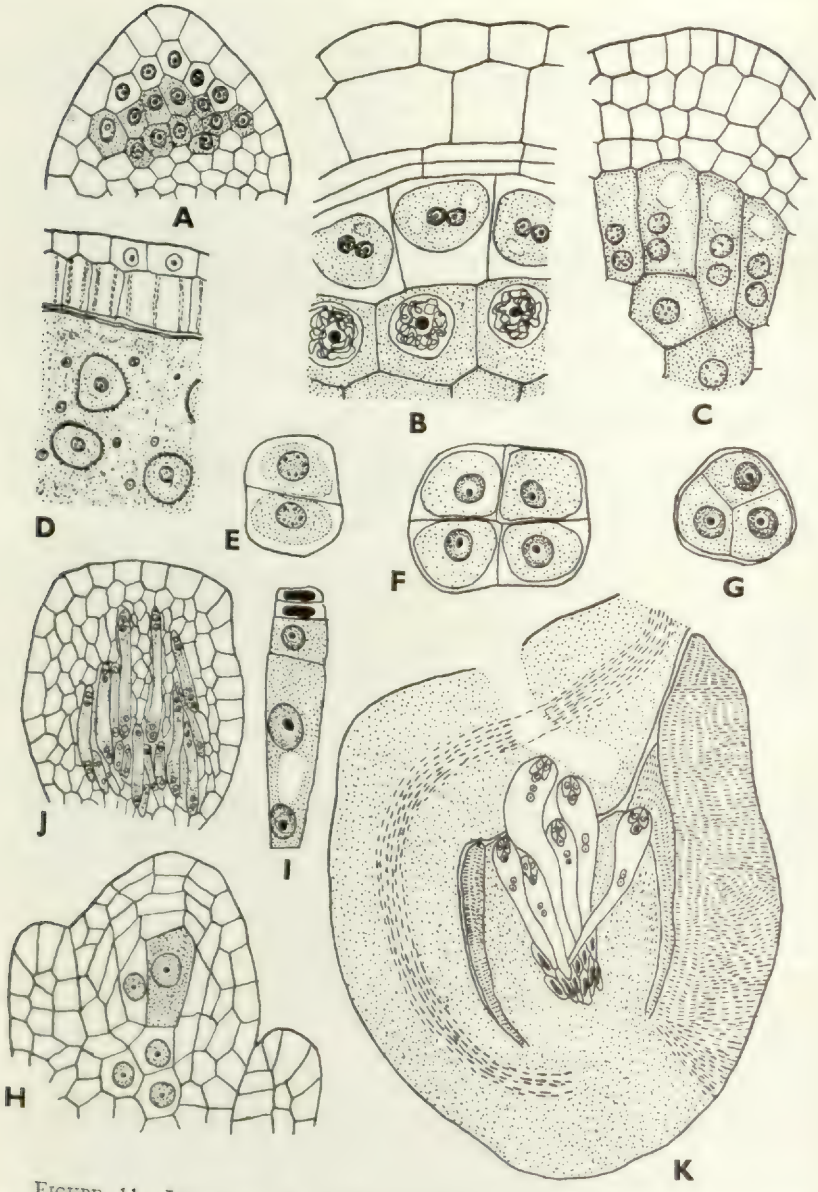

FIGURE 11. **Lauraceae.** A, Longisection of young ovule showing parietal layer and sporogenous cells. B, C, Transection of part of anther lobe, showing wall layers and tapetum. D, Longitudinal section of portion of anther lobe showing fibrous endothecium, periplasmodial tapetum, and uninucleate pollen grains. E–G, Stages in the successive type of cytokinesis and formation of tetrads. H, Longitudinal section of ovule showing megaspore mother cell. I, Linear tetrad, the micropylar two degenerated, the chalazal one at 2-nucleate stage. J, Longitudinal section of nucellus showing elongation of numerous em-

(FIGURES 11 H, J; 12 A, B). Numerous megaspore mother cells function (FIGURES 11 J; 12 A) in *Cassytha* (Sastri, 1962), and *Litsea* (Sastri, 1958). The chalazal megaspore of the linear tetrad functions (FIGURE 11 I) and gives rise to the Polygonum type of female gametophyte. Multiple embryo sacs are formed in *Cassytha* (FIGURES 11 J, K), although occasionally twin embryo sacs have been observed in *Persea americana* (Schroeder, 1952) also. In *Cassytha filiformis* tips of 4 to 6 embryo sacs elongate, bore through the nucellus, and finally lodge themselves in the funiculus or inner integument (FIGURE 11 K). The synergids degenerate soon after fertilization but in *Litsea iners* they persist for some time. The antipodal cells (*Cinnamomum, Sassafras, Umbellularia*) or nuclei (*Cassytha filiformis*) are ephemeral (FIGURE 11 K) but in *Laurus nobilis* they persist, divide, and form an antipodal complex (Mezzetti-Bambacioni, 1935).

In *Cassytha filiformis* the development of the endosporm is *ab initio* cellular (FIGURES 12 D, E), whereas in all other members it is nuclear (FIGURE 12 C). The cell formation in the nuclear endosperm takes place at 4-celled or globular stages of the embryo. In *Cassytha* the first and the next transverse division in the chalazal chamber results in 3-celled endosperm (FIGURE 12 D). The middle cell then undergoes a vertical division. Divisions in all planes result in a massive tissue (FIGURE 12 E) which comes out of the nucellus at its tip and plugs the micropyle. Haustorial structures commonly found in the parasitic angiosperms are not met with in *Cassytha*.

The development of the embryo conforms to the Piperad (*Sassafras*), Asterad (*Persea americana*), or Onagrad (*Cinnamomum iners* and *Litsea sebifera*) types. Orientation of walls at the four-celled stage is variable (FIGURES 12 F–I). The mature embryo has a well-developed radicle and a shoot apex which develops two small leaf primordia oriented at right angles to the two cotyledons (FIGURE 12 J).

In *Cinnamomum, Litsea*, and *Cassytha* the seed coat is formed by the outer integument alone and comprises an epidermis of radially elongated cells, a few parenchymatous layers, and an inner epidermis of elongated cells having helical thickenings (FIGURE 12 L). The pericarp comprises an epidermis of tannin-filled cells, a fleshy zone of 7 to 9 layers of parenchymatous cells, a single layer of radially elongated cells, and an inner epidermis of lignified and pitted columnar cells. In *Cinnamomum* and *Litsea* an additional 4- or 5-layered zone of stone cells is also present beneath the outer tanniniferous epidermis.

Nearly seven genera out of 31 included in the family have been worked out cytologically (Chung *et al.*, 1963; Darlington & Wylie, 1955; Hair & Beuzenberg, 1960; Mangenot & Mangenot, 1957, 1958; Sharma & Bhatt, 1959; Suzuka, 1953). The genera *Beilschmiedia* (3 spp.), *Cinnamomum*

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bryo sacs. K, Longitudinal section of ovule showing mature embryo sacs, two abutting the lysigenous cavity. (A, B, E–G, I–K, *Cassytha filiformis*; C, *Cinnamomum iners*; D, E, *C. zeylanicum*, after Sastri, 1958, 1962.)

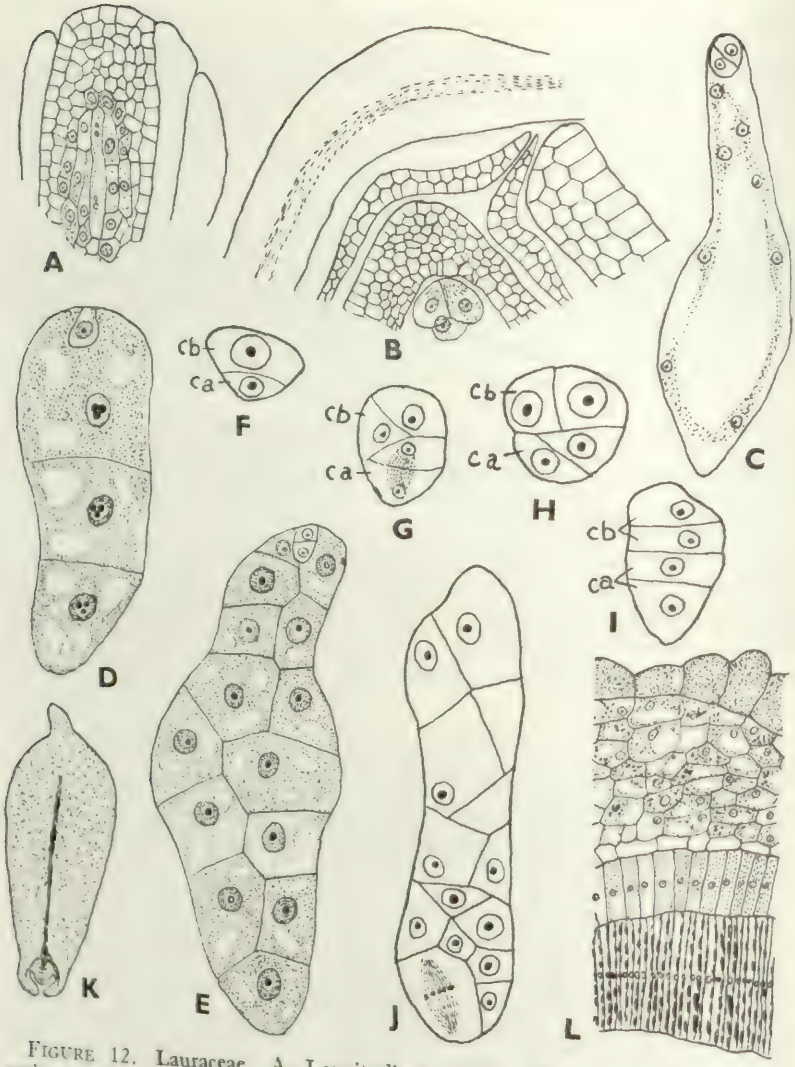

FIGURE 12. **Lauraceae.** A, Longitudinal section of ovule at four-nucleate embryo sac stage showing nucellar cells with prominent nuclei. B, Longitudinal section of apical region of ovule showing micropyle and egg apparatus. C, Longitudinal section of embryo sac showing endosperm nuclei and two-celled proembryo. D, E, Development of cellular endosperm. F–J, Stages in embryogenesis. K, Mature embryo in paracotyledonary view showing primordia of first two leaves. L, Longitudinal section of part of seed coat. (A–C, *Cinnamomum iners*; D–L, *Cassytha*, after Sastri, 1958, 1962.)

(9 spp.), *Lindera* (4 spp.), *Persea* (4 spp.), *Sassafras* (1 sp.), and *Umbellularia* (1 sp.) all possess $n = 12$. Only *Laurus* shows $2n = 36$ in *L. canariensis* and $2n = 42, 48$ in *L. nobilis*. The basic number of the family perhaps may be $x = 12$.

Trochodendraceae. Trochodendraceae is a monotypic family comprising *Trochodendron aralioides* distributed in Japan and Formosa.

Bailey and Nast (1945), and Nast and Bailey (1945) have studied the vegetative anatomy and floral morphology of *T. aralioides*, whereas Yoffe (1962, 1965) has investigated its embryology.

At the microspore-mother-cell stage the anther wall consists of an epidermis, the endothecium, two or three middle layers, and a two-layered glandular tapetum having binucleate cells (FIGURE 13 A). During maturation the epidermal cells of the anther wall become protuberant and develop cuticular fibrillar projections along their outer surface (FIGURE 13 B). The endothecium becomes very prominent by developing broad bands of fibrous thickenings; the middle layers become flattened and crushed. The tapetum, however, persists during the complete meiotic process in the microspore mother cells until the formation of two-celled pollen grains (FIGURE 13 B). At this stage the tapetal layer adjacent to the middle layers degenerates, whereas the one next to it develops Ubisch granules along the lateral and inner walls of the tapetal cells (FIGURE 13 B). Meiosis is normal but occasionally, a cell plate is formed during telophase I which, however, disappears later. The cytokinesis is of the simultaneous type and the resulting tetrads are tetrahedral. The nucleus of the microspore moves towards one side where it divides to form the generative and the vegetative cells. The mature pollen grains are 2-celled and tricolpate having a reticulate exine.

The ovules are anatropous, bitegmic, and crassinucellate (FIGURE 13 C). The inner integument is initiated first, followed by the outer, but the micropyle is formed by the inner integument alone (FIGURE 13 C). At the mature embryo-sac stage, the chalazal end of the ovule is transformed into a well-developed long, tapering projection. The vascular supply of the ovule enters this projection and curves backwards to end at the base of the chalazal region (FIGURE 13 C).

A single hypodermal archesporial cell cuts off a parietal cell which divides repeatedly to form a 3- or 4-layered parietal tissue. After meiosis I a dyad is formed which subsequently develops into either a T-shaped or linear tetrad. The chalazal megaspore functions (FIGURE 13 D) to give rise to a 2-nucleate, 4-nucleate (FIGURE 13 E) and 8-nucleate embryo sac of the Polygonum type (FIGURE 13 F). The synergids possess a conspicuous filiform apparatus; the antipodal cells are uninucleate and persistent (FIGURE 13 F).

Syngamy and triple fusion occur simultaneously. The development of the endosperm is *ab initio* cellular. The first division is transverse giving rise to a large micropylar and very small chalazal chamber (FIGURE 13 G). The next division in the micropylar chamber is transverse, while in the chalazal chamber it is vertical (FIGURE 13 H). Repeated divisions in both the chambers result in a massive endosperm tissue. However, the cells formed in the chalazal chamber are small and densely cytoplasmic. The major part of the endosperm tissue is formed by the micropylar chamber (FIGURE 13 I).

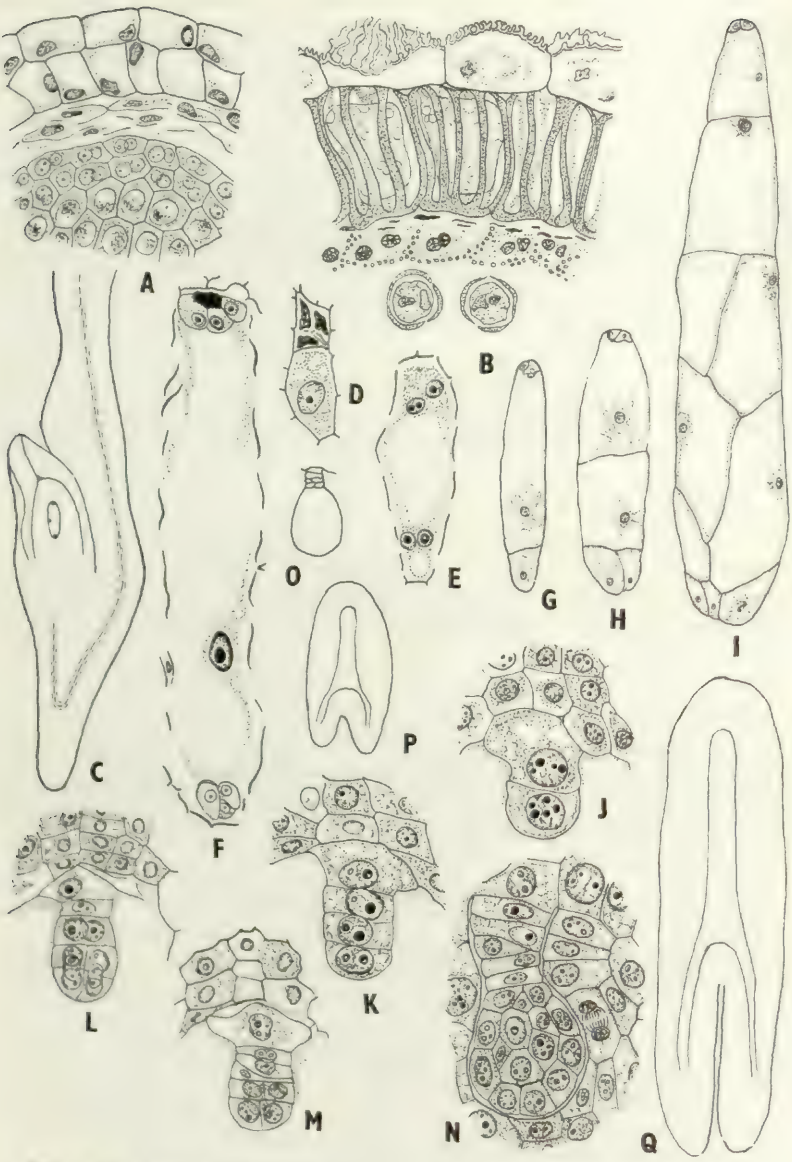

FIGURE 13. **Trochodendraceae.** A. Transection of part of anther lobe at microspore-mother-cell stage. B. Same, at time of dehiscence of anther — note cuticular protuberances in epidermis. C. Longisection of ovule at mature embryo sac stage, note circumscutous vascular supply. D. Tetrad of megaspores, upper three degenerated and chalazal megaspore functional. E. Four-nucleate embryo sac. F. Mature embryo sac. G–I. Stages in development of endosperm. J–Q. Stages in development of a dicot embryo. (A–Q. after Yoffe, 1962, 1965.)

The zygote divides transversely forming the two cells, *ca* and *cb* (FIGURE 13 J). Subsequent division in both these cells is transverse thus resulting in a 4-celled linear proembryo (FIGURE 13 K). The terminal cell of this proembryo divides vertically followed by another similar division at right angles to the first. The four cells thus formed divide transversely to form the octant disposed in 2 tiers of 4 cells each (FIGURE 13 L). Repeated divisions in this octant give rise to a globular proembryo (FIGURE 13 N, O). By this time the other 3 cells divide transversely and longitudinally and produce a suspensor (FIGURE 13 N). The globular proembryo differentiates first into a heart-shaped and later into a dicotyledonous embryo (FIGURE 13 P). At this stage the procambial strand is well developed (FIGURE 13 Q).

The seed coat is formed by both the integuments. In the mature seed the inner epidermis of the outer integument becomes thick-walled and sclerenchymatous to constitute the hard part of the seed coat whereas the other layers of the two integuments remain thin-walled. In the mature seeds the tapering chalazal projection becomes transformed into the wing.

The basic number of this monotypic family also is $n = 19$ in *Trochodendron aralioides* (Whitaker, 1933).

Cercidiphyllaceae. The genus *Cercidiphyllum*, which includes two species, *C. japonicum* and *C. magnificum*, constitutes the family Cercidiphyllaceae having a restricted distribution in Japan and China.

Swamy and Bailey (1949) have investigated the morphology, anatomy, and embryology of *Cercidiphyllum japonicum*. The structure and development of the anther resembles the majority of dicotyledons. The tapetum is, however, glandular with binucleate cells. The process of cytokinesis after reduction divisions is of the simultaneous type resulting in microspore tetrads. The pollen grains at the shedding stage are 2-celled, spherical, and tricolpate; the colpi are conspicuously broad. The exine is finely pitted.

The ovules are hemianatropous, bitegmic, and crassinucellate. The two integuments are initiated almost at the same time; the outer integument soon overgrows the inner, although in a mature ovule both the integuments take part in the formation of micropyle. The chalazal end of the ovule develops into a flattened tapering projection which forms a wing in the mature seed. After fertilization the vascular bundle reaches the middle of the tapering chalazal projection and then bends to end at the base of the nucellus.

The female archesporium is single-celled, forming five or six parietal cells (FIGURE 14 A). Periclinal divisions in the nucellar epidermis add to the formation of a massive parietal tissue, resulting in a deeply seated megaspore mother cell in the nucellus (FIGURE 14 A). The megaspore mother cell undergoes meiosis thus giving rise to a linear tetrad. The three micropylar megaspores degenerate while the chalazal one functions (FIGURE 14 A) to form an eight-nucleate embryo sac of the Polygonum type (FIGURE 14 B). The egg apparatus is conspicuous, three antipodal

cells are uninucleate while the two polar nuclei fuse before fertilization (FIGURE 14 B).

The primary endosperm nucleus moves to the chalazal part of the embryo sac where it divides, followed by formation of a transverse wall resulting in a large micropylar and a small chalazal chamber (FIGURE 14 C). Subsequent divisions in the two chambers are essentially transverse until a 10- to 12-celled uniseriate endosperm is formed (FIGURE 12 D). During this growth period the embryo sac enlarges considerably and comes to be in close contact with the vascular strand (FIGURE 14 F). Further divisions occur in all planes finally producing a compact mass of endosperm tissue (FIGURE 14 E), most of which, however, is consumed by the developing embryo.

The zygote divides transversely to form the cells *ca* and *cb*. The basal cell *cb* enlarges conspicuously without undergoing any further divisions (FIGURE 14 G); whereas the terminal cell *ca* divides again transversely (FIGURE 14 H). Subsequent divisions in the derivatives of the terminal cell are vertical to organize the quadrant and octant (FIGURES 14 I, J). The cells of the octant divide further and form a globular proembryo (FIGURES 14 K, L). In the mature seed the embryo possesses a long hypocotyl and two cotyledons which enclose the embryonal shoot apex. The embryogeny, therefore, is of the Solanad type.

The seed coat is formed by the outer integument alone. In the region of the wing it becomes flattened so that the chalazal wing appears to extend beyond it at either side.

Of the two species of *Cercidiphyllum* included, chromosome counts have been made for *C. japonicum*, which is $n = 19$ (Whitaker, 1933). No karyotypic analysis is available.

MORPHOLOGY AND ANATOMY

A comparative study of the morphology and anatomy of the ranalian families has yielded many fundamental concepts and their further phylogenetic amplification. The work is exhaustive and voluminous and will not be repeated here for want of space. For detailed information the reader is referred to the chief publications on Magnoliaceae (Canright, 1952, 1953, 1955, 1960, 1963, 1965; Lemesle, 1933, 1953; McLaughlin, 1933; Ozenda, 1913; Tucker, 1959, 1961), Winteraceae (Bailey, 1944a, b; Bailey & Nast, 1943a,b, 1944a,b, 1945; Tucker, 1960), Degeneriaceae (Swamy, 1949), Himantandraceae (Bailey, Nast & Smith, 1943), Wettstein, 1935; Wilson, 1960, 1964, 1965; Vestal, 1935, Annonaceae (Wyk & Canright, 1956; Ozenda, 1947), Eupomatiaceae (Lemesle, 1938), Myristicaceae (Garrat, 1933a,b; Nair & Bahl, 1956), Canellaceae, Schisandraceae (Bailey & Nast, 1948; Jalan, 1968; Smith, 1947), Illiciaceae (Bailey & Nast, 1948; Lemesle, 1945; Smith, 1947), Austrobaileyaceae (Bailey & Swamy, 1949), Trimeniaceae, Amborellaceae, and Monimiaceae (Bailey & Swamy, 1948; Money, Bailey, & Swamy, 1950), Calycanthaceae (Fahn & Bailey, 1957; Smith, 1928), Gomortegaceae (Money, Bailey, & Swamy,

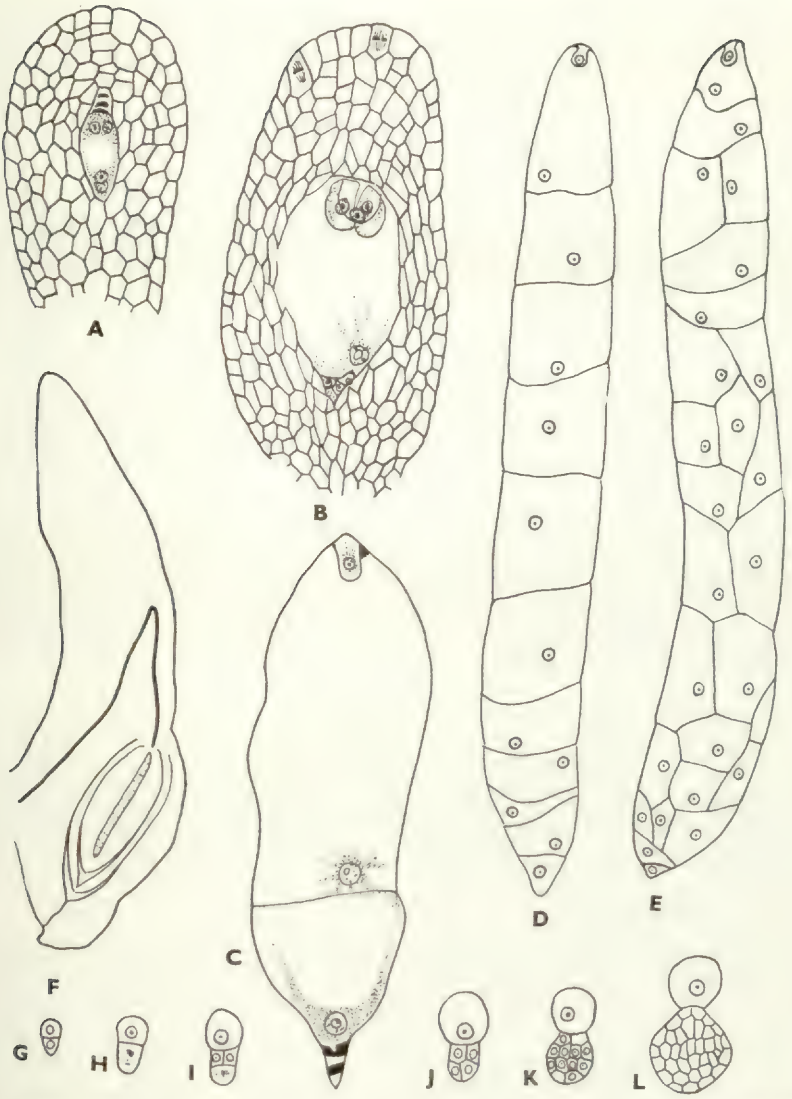

FIGURE 14. **Cercidiphyllaceae.** A, Longitudinal section of nucellus showing four-nucleate embryo sac. B, Same, showing mature embryo sac. C–E, Stages in development of endosperm. F, Longitudinal section of ovule showing early stages in formation of endosperm. G–L, Stages in development of the embryo —note that basal cell does not divide and contribute much in formation of embryo proper. (A–L, after Swamy & Bailey, 1949.)

1950), Lauraceae (Coy, 1928; Sastri, 1952; Stern, 1954), Hernandiaceae (Shutts, 1960), Tetracentraceae and Trochodendraceae (Bailey & Nast, 1945; Croizat, 1947; Nast & Bailey, 1945; Smith, 1947), and Cercidiphyllaceae (Swamy & Bailey, 1949). Eames (1961) has given an excellent

review on Ranales which outlines in brief, the principal trends of specializations in the group.

INTERRELATIONSHIPS

General considerations. ANTHER WALL. In almost all the families the basic architecture of the structure of the anther wall is uniform and comprises the epidermis, fibrous endothecium, 2 to 4 middle layers, and tapetum. The epidermis is persistent till the dehiscence of the anther: Trochodendraceae stands apart from the rest of the families in having prominent fibrillar cuticular thickenings on the outer surface. The fibrous endothecium (excepting *Magnolia stellata*; Kapil & Bhandari, 1964) is persistent and mostly 1-layered. However, in Magnoliaceae (Hayashi, 1960; Kapil & Bhandari, 1964; Padmanabhan, 1960), Degeneriaceae (Swamy, 1949), Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968; Swamy, 1949), and Schisandraceae (Kapil & Jalan, 1964), there is a tendency for it to become irregularly 2-layered along the outer face of the anther wall while some layers of the connective tissue toward the inner side also develop fibrous thickenings and simulate the endothecium. Its maximum amplification is found in the relatively more primitive families Winteraceae and Degeneriaceae, and perhaps indicates that it is a primitive feature and that the phylogenetic trend proceeds toward the reduction of the endothecial tissue.

The middle layers vary from 2 to 4 in number and again in Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Illiciaceae, and Canellaceae 1 or 2 middle layers persist even at the time of dehiscence of the anther, whereas there is a decrease in the number of the middle layers in Myristicaceae, Monimiaceae, Lauraceae, and Trochodendraceae. They are ephemeral and become completely crushed during and after meiosis in Myristicaceae, Lauraceae, and Trochodendraceae.

ANTHER TAPETUM. The families Austrobaileyaceae, Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Myristicaceae, Canellaceae, Schisandraceae, Illiciaceae, Monimiaceae, Calycanthaceae, Trochodendraceae, and Cercidiphyllaceae resemble each other in having glandular tapetum. In *Annona* (Juliano, 1935; Asana & Adatia, 1947) and *Polyalthia*, *Unona*, and *Cananga* (*see* Asana & Adatia, 1947) of the Annonaceae, most Lauraceae excepting *Cassytha* (Sastri, 1962), and *Pseudowintera colorata* (Bhandari, 1963c) of the Winteraceae, amoeboid tapetum has been reported. The occurrence of amoeboid tapetum in the Annonaceae is questioned by Periasamy and Swamy (1959) first because of lack of proper illustrations in the works of Juliano (1935) and Asana and Adatia (1947), and because they found glandular tapetum in *Cananga odorata* whereas Asana and Adatia (1947) had earlier reported amoeboid tapetum in this species. It may turn out that Annonaceae have only glandular tapetum. Of the three genera of the Winteraceae investigated, *Drimys*, *Pseudowintera*, and *Zygogynum*, only one species, *Pseudowintera colorata* (Bhandari, 1963c) possesses amoeboid tapetum. The other species *P. axillaris*

(Sampson, 1963) has glandular tapetum. Furthermore, an earlier report of amoeboid tapetum in *Drimys* (Kutti Amma, 1938) has been refuted recently by Bhandari and Venkataraman (1968). Therefore, Lauraceae is the only family where amoeboid tapetum can be regarded as a family character.

Glandular tapetum, therefore, reflects a primitive pattern whereas the amoeboid tapetum is a phylogenetic departure. In the Ranunculales, the herbaceous Ranales, a parallel trend can also be observed, although the amoeboid tapetum occurs more frequently in this group.

In Magnoliaceae and Trochodendraceae the glandular tapetum is bilayered while in Schisandraceae and Illiciaceae it becomes irregularly bilayered. In the rest of the families it is uniformly 1-layered. The presence of Ubisch granules binds the Magnoliaceae, Trochodendraceae, and Canellaceae together. In the last family, however, the granules are studded along the inner as well as outer faces of the tapetal walls. The cells of the tapetum are uninucleate in Myristicaceae, binucleate in Magnoliaceae, Degeneriaceae, Annonaceae, Illiciaceae, Trochodendraceae, and Cercidiphyllaceae, and multinucleate in Magnoliaceae, Annonaceae, Canellaceae, Schisandraceae, Monimiaceae, and Lauraceae with a tendency to form polyploid nuclei by fusion.

Origin of tapetum. The sporogenous origin of the tapetum has been looked at suspiciously and this was particularly true in some instances since a reinvestigation proved its parietal origin at least along the outer (protuberant) face of the anther locule (*see* Maheshwari, 1950). Recently, Swamy and Periasamy (1966) argued that the tapetum is of dual origin, contributed by parietal tissue along the outer side, and by the connective or septal tissue along the inner side of the locule (*see also* Coulter & Chamberlain, 1905). This conclusion has been further supported by ontogenetic studies of anther wall development in *Anemone rivularis* (Bhandari, 1968). Bhandari (1968) has suggested a reappraisal of the sporogenous origin of tapetum and it may be in some instances that this tissue does change its function from reproductive to nutritional as is the case in most of the gymnosperms. Such a situation has been observed in Annonaceae. In *Annona* (Juliano, 1935), *Cananga odorata*, and *Miliusa wightiana* (Periasamy & Swamy, 1961) the microspore mother cells are separated by septae which originate from the sporogenous tissue and behave like the tapetum developing from the parietal tissue. In such members of Annonaceae, therefore, the tapetum is contributed partly by the sporogenous tissue and partly by the parietal tissue. Hayashi (1960) has reported sporogenous origin of the tapetum in *Magnolia liliflora* and *M. virginiana*. The Magnoliaceae and Annonaceae thus share this feature.

Cytokinesis and microspore tetrads. Cytokinesis in microspore mother cells at the end of the first or second meiotic division is another important character. It is simultaneous in Austrobaileyaceae, Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae (some members), Canellaceae, Schisandraceae, Illiciaceae, Monimiaceae, Calycanthaceae Trochodendraceae, and Cercidiphyllaceae, whereas in Annonaceae (some members),

Myristicaceae, and Lauraceae it is of the successive type. Sastri (1957) is of the opinion that in Annonaceae a series exists from the successive type of cytokinesis in *Annona reticulata*, *Asimina triloba*, and *Uvaria kirkii* to the simultaneous type in *Saccopetalum tomentosum* and *Polyalthia*, through intermediate types like *Annona cherimolia* and *A. squamosa* where the first constriction, although initiated at the end of heterotypic division, is delayed, and completed only along with the other after the homotypic division. A similar situation is also met with in *Magnolia* (Kapil & Bhandari, 1964, *see also* Farr, 1918), *Zygogynum baillonii* (Swamy, 1952) of the Winteraceae, and *Trochodendron* (Yoffe, 1962). Periasamy and Swamy (1959) on the other hand, consider the successive type of cytokinesis of the Annonaceae to be of modified simultaneous type. The present author is not in agreement with Periasamy and Swamy (1959) and considers that if a dyad is formed at the end of the heterotypic division as in *Asimina* and *Uvaria*, it should be regarded as the successive type irrespective of its formation, by cell plate or by furrowing. The preponderance of the simultaneous type of cytokinesis in the majority of the Magnolian taxa and the occurrence of the intermediate forms where the first furrow is initiated after heterotypic division, together with the formation of an evanescent cell plate in primitive genera like *Zygogynum baillonii* (Swamy, 1952), *Pseudowintera axillaris* (Sampson, 1963), *Drimys winteri* (Bhandari & Venkataraman, 1968), and *Magnolia* (Kapil & Bhandari, 1964) might indicate that the successive type is a derived condition (*see also* Maheshwari, 1950).

At the end of meiosis tetrahedral tetrads are formed in Canellaceae, Illiciaceae, Monimiaceae, and Trochodendraceae, and tetrahedral or decussate tetrads in the Magnoliaceae, Winteraceae, Schisandraceae, Calycanthaceae, and Cercidiphyllaceae. Tetragonal tetrads are found in Degeneriaceae and Annonaceae, while in Myristicaceae only the isobilateral type occurs. In the Lauraceae, tetrahedral, isobilateral, linear, or T-shaped types of tetrads are met. Two trends are evident: (1) the retention of the microspores within the microspore mother cell until they are partially mature and their delayed release as in Degeneriaceae (Swamy, 1949) and Canellaceae (Parameswaran, 1962); and (2) the shedding of the pollen grains in permanent tetrads as in Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968), Lactoridaceae, and occasionally also in Annonaceae (*see* Parulekar, 1967), and Magnoliaceae (Canright, 1953).

Generative cell. In all the families the pollen grains are shed at the two-celled stage. The mode of cutting off of the generative cell is very specific but at the same time very difficult to ascertain since the division of the microspore nucleus takes place after they are released from the tetrads. In the Austrobaileyaceae, Degeneriaceae, Annonaceae, and in abnormal tetrads of *Magnolia* (Canright, 1962), the generative cell is cut off towards the distal pole, while in Winteraceae and Canellaceae it is formed towards the proximal end. In Degeneriaceae and Canellaceae, however, the microspores become two-celled within the tetrads.

Ovule. The ovules are anatropous, bitegmic, and crassinucellate in

Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Myristicaceae, Schisandraceae, Illiciaceae, Monimiaceae, Calycanthaceae, Lauraceae, Trochodendraceae, and Cercidiphyllaceae. In some members of Annonaceae, however, the ovules are tritegmic and in Canellaceae they may also be hemianatropous. In *Siparuna* of the Monimiaceae the ovules are unitegmic. In the Magnoliaceae, Degeneriaceae, and Annonaceae the outer integument is vascularized whereas in others, the funicular supply ends at the base of the nucellus. The micropyle is formed by both the integuments in Magnoliaceae, Annonaceae, Canellaceae, Schisandraceae, Illiciaceae, Lauraceae, and Cercidiphyllaceae while in Degeneriaceae, Winteraceae, Myristicaceae, Monimiaceae, Calycanthaceae, and Trochodendraceae it is formed by the inner integument. The micropyle is zigzag in Canellaceae, whereas it is straight in the other families. The family Trochodendraceae (Yoffe, 1965) and Cercidiphyllaceae (Swamy & Bailey, 1949) resemble each other in having a chalazal tapering projection; the funicular vascular supply enters the projection for some distance and then bends back to end at the base of the nucellus. This projection forms a wing-like structure in the seed.

The massive parietal tissue is formed by the parietal cell alone in Magnoliaceae, Degeneriaceae, Winteraceae, Annonaceae, Schisandraceae, Illiciaceae, and Trochodendraceae. In Monimiaceae and Cercidiphyllaceae it develops from both the primary parietal cell and the nucellar epidermis, while in Calycanthaceae it originates from nucellar epidermis alone. The family Lauraceae, however, exhibits both the trends where the parietal tissue is formed by the parietal cell alone or together with the nucellar epidermis. Although the relic feature of producing a massive parietal tissue is retained, the evident phylogenetic trend is towards the suppression of the formation of this tissue from the primary parietal cell, a trend which becomes well established in some of the herbaceous ranalian families such as Ranunculaceae (some members), Berberidaceae, Lardizabalaceae, and some members of Menispermaceae (*see* Bhandari, 1962, 1963b, 1965, 1968; Bhatnagar, 1965; Johri, 1936; Joshi, 1939; Sastri, 1964; Swamy, 1953). A prominent nucellar cap is met with in Monimiaceae, Calycanthaceae, and Lauraceae (Heilborn, 1931; Mauritzon, 1935; Sastri, 1963; Schnarf, 1931). A conspicuous hypostase is met with in Magnoliaceae (Kapil & Bhandari, 1964), Degeneriaceae (Swamy, 1949), Annonaceae (Corner, 1949), and Monimiaceae (Mauritzon, 1935).

MEGASPOROGENESIS AND FEMALE GAMETOPHYTE. The female archesporium is hypodermal, 1-celled in the families Degeneriaceae (Swamy, 1949), Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968; Sampson, 1963; Swamy, 1952), Myristicaceae (Schnarf, 1931), Canellaceae (Parameswaran, 1962), Illiciaceae (Yoshida, 1962), Trochodendraceae (Yoffe, 1965), and Cercidiphyllaceae (Swamy & Bailey, 1949) but multicelled in Schisandraceae (Kapil & Jalan, 1964; Yoshida, 1962), Calycanthaceae (Schnarf, 1931), and Lauraceae (Sastri, 1963). In the Magnoliaceae (Kapil & Bhandari, 1964; Padmanabhan, 1960), Annonaceae (Parulekar, 1967), and Monimiaceae (Heilborn, 1931; Mauritzon, 1935) the archesporium may be 1- to multicelled. The tendency, however,

is towards the reduction in the number of archesporial cells as is evident in Magnoliaceae (Kapil & Bhandari, 1964) where, although numerous archesporial cells differentiate, ultimately only one functions. Only in the Lauraceae and Calycanthaceae do large numbers of megaspore mother cells function simultaneously, these have perhaps retained the ancestral feature of forming functional massive sporogenous tissue. In *Siparuna* of the Monimiaceae (Heilborn, 1931) the ovules are unitegmic but have a multicelled archesporium, a combination of advanced and primitive features.

In almost all the families the development of the female gametophyte conforms to the Polygonum type. In *Schisandra grandiflora* (Kapil & Jalan, 1964) and *Schisandra chinensis* (Yoshida, 1962), the Polygonum type of female gametophytes has been reported, whereas Swamy (1964) observed the Oenothera type, and a unique bisporic type (organizing after 4-nucleate stage) in *S. chinensis*. The Allium type of embryo sac has also been recorded in *Peumus boldus* (Mauritzon, 1936) of the Monimiaceae. It is evident, therefore, that although wall formation takes place after meiosis I and II, resulting in a tetrad of megaspores in a majority of the Magnolian members, there is a tendency towards suppression of the cytokinesis after homotypic division, hence towards a bisporic type.

The synergids and the antipodal cells or nuclei (*Cassytha*, Sastri, 1962) are characteristically ephemeral excepting in *Peumus* where secondary multiplication occurs to form the antipodal cell complex. The polar nuclei fuse before fertilization, which is porogamous. Multiple embryo sacs are reported in Lauraceae (Sastri, 1962), occasionally twin embryo sacs are met with in *Magnolia* (Kapil & Bhandari, 1964) and *Drimys winteri* (Bhandari & Venkataraman, 1968). Embryo sac haustoria are found only in *Cassytha* (Sastri, 1962).

Endosperm. The endosperm is *ab initio* cellular in the Magnoliaceae (Kapil & Bhandari, 1964; Padmanabhan, 1960), Degeneriaceae (Swamy, 1949), Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968), Annonaceae (Periasamy & Swamy, 1958), Schisandraceae (Kapil & Jalan, 1964), Illiciaceae (Hayashi, 1963), Monimiaceae (Mauritzon, 1935), Calycanthaceae (Schnarf, 1931), *Cassytha* (Sastri, 1962), Trochodendraceae (Yoffe, 1965), and Cercidiphyllaceae (Swamy & Bailey, 1949). The endosperm is nuclear only in Myristicaceae and Lauraceae (excepting *Cassytha*). In Calycanthaceae its development is reported to be autonomous. The division of the primary endosperm nucleus is transverse (rarely vertical in *Pseudowintera colorata*, *see* Bhandari, 1963c) and even further segmentation is very characteristic and similar in a large number of Magnolian members, thus producing a uniseriate file of cells. Later, divisions in all planes result in a massive endosperm tissue. *Magnolia obovata* (Kapil & Bhandari, 1964) is the only record of the presence of a 2- or 3-celled chalazal endosperm haustorium. The families Degeneriaceae (Swamy, 1949), Annonaceae (Corner, 1949; Periasamy & Swamy, 1961), Myristicaceae (Periasamy, 1961), and Canellaceae (Parameswaran, 1961) resemble each other in having ruminate endosperm. However, the tissue causing rumination is histologically different in various families. In De-

generiaceae (Swamy, 1949) and Annonaceae (Periasamy, 1962; Periasamy & Swamy, 1961) the ruminating projections develop from the outer integument, while in Myristicaceae (Periasamy, 1961) they originate from the meristematic chalaza. For Canellaceae (Parameswaran, 1961), however, such details are not known.

The presence of cellular endosperm in most members of the Magnoliales and allies seems to indicate the primitiveness of this feature, and the restricted occurrence of the nuclear type may be a phylogenetic advancement. This is also confirmed by the fact that in the Ranunculales most herbaceous members have nuclear type. The presence of a haustorium which is not very aggressive is inexplicable; whether this is the preservation of a relic feature or a phylogenetic advancement which was to be well established in many other groups of angiosperms remains highly speculative. The latter possibility appears to be more sound.

Embryogeny. In some members of Magnoliaceae (Kapil & Bhandari, 1964), Degeneriaceae (Swamy, 1949) and Winteraceae (Bhandari & Venkataraman, 1968) the early segmentation is rather irregular, although at the preglobular or globular stages the embryogenesis proceeds normally and forms a healthy embryo. In other families, wherever information is available, the pattern of development becomes established and is mostly of the Onagrad (Annonaceae), Onagrad or Asterad (Schisandraceae, Lauraceae), Asterad (Illiciaceae, Monimiaceae), or Solanad type (*see* Davis, 1966). However, one basic factor evident throughout is that the basal cell, *cb*, has little or no role in the organization of the embryo proper and forms the major part of the suspensor.

Seed coat. In the Magnoliaceae, Winteraceae, Degeneriaceae, Annonaceae, Myristicaceae, Lauraceae, and Cercidiphyllaceae the seed coat is constituted chiefly by the outer integument while the inner intgument degenerates and its remnants may persist. In Canellaceae, Schisandraceae, and Trochodendraceae, however, both the integuments take part in formation of the testa. In the Magnoliaceae and Degeneriaceae the seed coat is differentiated into outer fleshy and inner stony regions but in the rest of families the seed possesses a hard seed coat. In the Winteraceae it is mostly the enormously radially elongated outer epidermis which constitutes the seed coat while the rest of the layers become slightly thick walled. In Canellaceae and Trochodendraceae the outer epidermis of the outer integument and the inner epidermis of the inner integument become sclerenchymatous whereas the rest of the layers remain thin walled. The Schisandraceae possess an elaborate seed structure (*see* Kapil & Jalan, 1964), having outer integument comprising the epidermis of macrosclereids, 2 or 3 subepidermal layers of brachysclereids, and 2 or 3 parenchymatous layers. The inner integument also persists as a thin layer of degenerated thick-walled cells. In Degeneriaceae, Myristicaceae, Canellaceae, and Annonaceae the ruminations in the seed are produced by the outer integument. The Trochodendraceae and Cercidiphyllaceae possess a tapering chalazal projection which develops into a wing-like structure in the mature seed.

[*To be continued*]

THE GENERA OF THE URTICACEAE IN THE SOUTHEASTERN UNITED STATES[1]

NORTON G. MILLER

URTICACEAE A. L. de Jussieu, Gen. Pl. 400. 1789, "Urticae," nom. cons.
(NETTLE FAMILY)

Taprooted and rhizomatous annual and perennial herbs [or shrubs, rarely large trees], with watery [rarely milky] sap, generally provided with a vesture of some kind, sometimes with stinging hairs. Stems often fluted, mostly nonsucculent, but sometimes fleshy or translucent. Leaves alternate or opposite, sometimes anisophyllous, simple, usually petiolate, blades mostly ovate to lanceolate [rarely lobed]; punctiform, linear [or stellate] cystoliths borne in cells of the adaxial (upper) or abaxial (lower) epidermis or both; margins serrate, dentate, entire, or rarely incised, venation pinnate or palmate; stipules present or absent, if present, either paired at the petiole base or intrapetiolar and partly to entirely connate, fugacious or not. Plants monoecious, dioecious, or polygamous; flowers imperfect, rarely perfect; inflorescences basically cymose, axillary, bracteate, the flowers arranged in loose to tight clusters, or inflorescence sometimes racemose or paniculate [or flowers aggregated on a flat or campanulate to figlike receptacle]; if monoecious, staminate and carpellate flowers in different inflorescences or intermingled. Staminate flowers small, greenish or whitish, rarely otherwise, with short pedicels or sessile, caducous after shedding pollen; tepals 4, 5 [6], equal, valvate, or partly fused

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before anthesis [sometimes appendaged]; stamens of equal number and opposite the perianth segments [or a single stamen and a subtending involucre]; filaments initially inflexed, slightly flattened, pollen dispersal explosive as the stamens free themselves from the partially surrounding tepals; anthers 2-locular at anthesis, medifixed, thin walled, reniform, oriented with the concave sides inward, dehiscence longitudinal; pollen with 2, 3, or 4[–6] pores, ± suboblate, exine stratification obscure, equatorial diameter ca. 15 μ; rudimentary gynoecium prominent, conical, obovoid, globose, or cup-like, hyaline or not, glabrous [or woolly]. Carpellate flowers minute, sessile or subsessile, greenish or reddish; tepals 3 or 4 or perianth ± tubular [or rarely absent]; staminodia present or absent; gynoecium unicarpellate; style 1, present or absent, if present, apical at anthesis and rarely becoming laterally displaced in fruit; stigma penicillate, linear, or style prolonged into a filiform stigma; ovule 1, basal, usually orthotropous, sometimes hemianatropous, bitegmic, crassinucellar. Perfect flowers with 4 basally fused tepals and 4 opposite stamens, gynoecium with a penicillate or linear stigma. Fruits mostly laterally compressed or ovoid, symmetrical to asymmetrical achenes, rarely drupaceous, generally either loosely or tightly surrounded by the accrescent perianth [which becomes fleshy in some], achene and perianth sometimes dispersed as a unit; style and stigma persistent or not. Seed 1, seed coats thin, brownish, membranaceous; endosperm thin, fleshy or mealy, completely surrounding the embryo; embryo straight, radicle pointing toward the ovary apex and shorter to longer than the orbicular to ovate, sometimes emarginate, cotyledons. Embryo sac development of the Polygonum type; embryogeny of the Asterad type. TYPE GENUS: *Urtica* L.

A natural family of about 40 genera and 800 species (ca. 1900 according to Hutchinson), largely confined to tropical and subtropical latitudes of both New and Old Worlds, rarer in temperate regions, and represented by only a few species still farther poleward. Of the six genera native to the United States (excluding Hawaii with four additional genera, two of which, *Neraudia* Gaud., with milky sap, and *Touchardia* Gaud., are endemic), five have one or more species in our region. Closely related to *Urtica*, but differing in the continuous, appressed perianth of the carpellate flower, *Hesperocnide* Torr. occurs in California (*H. tenella* Torr.) and Hawaii (*H. sandwicensis* Wedd.; however, see W. Hillebrand, Fl. Hawaii. Is. 408. 1888, who regards the Hawaiian plants as probably unintentionally introduced from California at an early date).

The family has traditionally been divided into five tribes. Four have representatives in North America. Floral morphology in the exclusively Old World tribe Forskohleeae Gaud. is somewhat atypical for the family as a whole, in that staminate flowers are comprised of a single stamen and a subtending perianth (or involucre), while carpellate flowers may either have a perianth or lack one altogether. The other tribes are distinguished mainly on the nature of the perianth in both staminate and carpellate flowers. Only members of the Urticeae have stinging hairs. As has been

recently suggested, *Cecropia* L., *Coussapoa* Aubl., and *Musanga* C. Sm. ex R. Br., which generally have been placed in subfam. Conocephaloideae of the Moraceae, are better treated as a separate tribe of the Urticaceae on account of their basal, orthotropous ovules (cf. Chew, Corner). The oldest tribal name available for these genera would seem to be Cecropieae Gaud.

Wind pollination is characteristic of the family, and the staminate flowers are accordingly reduced and of a relatively simple form. However, the presence of vestigial nectaries, at least in flowers of *Urtica dioica*, is suggested by Stäger's work. Pollen is hurled into the air by an abrupt and often simultaneous extension of the inflexed filaments, which prior to anthesis are held in place by the tepals. Associated with the extension is a sudden bursting of the anther-sacs that may be related to the short longitudinal slit observed in the wall of the young anther (Eames), although the precise mechanism is not known. The uniseriate anther-sac walls of the Urticaceae seem to represent the endpoint of a reduction series in which epidermal and fibrous layers have been successively lost. Intermediate stages in the series are encountered in other members of the Urticales.

Anatomically, the family has been studied from several standpoints. Laticiferous canals have been found in stems and roots (sometimes both) in certain species of *Dendrocnide* Miq. and *Urera* Gaud., both members of tribe Urticeae. Mucilage cells similar to those occurring in the Tiliaceae are abundant in the stems and leaves of many genera. Bechtel's identification of aborted vascular bundles in gynoecia of *Laportea canadensis* and *Urtica gracilis* suggests that the unicarpellate ovary, which is usually cited as a family character, may have been derived through abortion of a second (and anterior) carpel. He has also presented evidence for a shift in ovule position from either the side or apex of the locule to its base. In *Boehmeria cylindrica* the vascular bundle supplying the ovule ascends the carpel wall for a short distance and later reverses direction to enter the ovule at the base of the ovary. Anatomical study of the tubular perianth of this species shows it to be comprised of two segments. Development of zygomorphic flowers (weakly expressed in *Urtica*, but obvious in *Laportea*) is a notable specialization of floral structure.

The occurrence of cystoliths (generally mineralized with calcium carbonate) supported by a cellulose stalk in enlarged epidermal cells of leaves and sometimes elsewhere is a characteristic feature of the Urticaceae, although similar ones are known in other families of the Urticales and in the Acanthaceae. Spherical, bacilliform, and fusiform (curved or straight) types are most common; stellate or vermiform shapes occur rarely. Cystoliths are difficult to see in living plants but are apparent in dried specimens as elevated markins.[2] Ashed leaf fragments containing cystoliths, calcium oxalate crystals, and calcified or silicified cell walls, have been studied

[2] Sreemadhavan *et al.* (Taxon 17: 17, 18. 1968) have introduced the term "furuncle" (*adj.* furunculate) to describe elevations in dried material arising from either cystoliths or raphides.

microscopically, either embedded in celloidin to preserve their original orientation and arrangement in the leaf (a spodogram), or as simple mounts of the ash residue. Cystoliths may be diagnostically useful at various taxonomic levels. There is a general correspondence between cystolith shape and tribes of the Urticaceae (e.g., members of the Elatostemeae Gaud. for the most part have linear cystoliths), and different species within a genus may have markings of distinctive shape.

Chromosome counts reported for 17 genera are $2n = 14$, 16, 20, 22, 24, 26, 28, 32, 42, 48, 52, 60, and 76–78.

The Urticaceae, Moraceae, Cannabaceae, and Ulmaceae (and perhaps the Barbeyaceae) are generally taken to comprise the Urticales whose derivation from the Magnoliales through the Hamamelidales is postulated by many workers. A relationship between the Urticaceae and certain families of the Malvales has been suggested also.

Apart from ramie (*Boehmeria nivea*), a fairly important fiber plant in the Orient, the family is of little importance economically. Several species of *Pilea* and *Pellionia* Gaud. are grown as ornamentals, and *Soleirolia soleirolii* (Req.) Dandy (*Helxine soleirolii* Req.), baby tears, $2n = 20$, a native of Corsica and Sardinia, is a favored houseplant.

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KEY TO THE GENERA OF THE URTICACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *monoecious, dioecious, and polygamous annual or perennial herbs, with or without stinging hairs; leaves stipulate or exstipulate, mostly opposite, but sometimes alternate, always with cystoliths; inflorescences cymose, axillary; flowers either staminate or carpellate, rarely perfect; staminate flowers with 4 or 5 tepals and an equal number of opposite stamens, rudimentary gynoecium present; perianth or carpellate flowers accrescent, either tubular or of 3 or 4 separate, equal or unequal tepals, staminodia rarely present; perfect flowers with 4 equal, mostly fused tepals, perianth accrescent; gynoecium unicarpellate, ovule one, basal, generally orthotropous; style one or absent, stigma generally*

penicillate or linear; fruits mostly achenes (rarely drupaceous), loosely to tightly surrounded by the persistent perianth or not.

A. Plants with stinging hairs; perianth of carpellate flowers at fruiting stage comprised of four separate tepals, 1 pair large, the other small.
  B. Leaves opposite; style absent, stigma apical, penicillate; achene erect, symmetrical, nonstipitate; pedicel supporting mature fruit short and wingless. ..... 1. *Urtica.*
  B. Leaves alternate; style and stigma awl-shaped, at first apical but displaced to a lateral position during fruit maturation; achene deflexed, asymmetrical, stipitate; pedicel supporting mature fruit long and bearing lateral wings. ..... 2. *Laportea.*

A. Plants without stinging hairs, otherwise pubescent or not; perianth of carpellate flowers at fruiting stage either tubular or of three separate tepals.
  C. Perianth of carpellate flowers with 3 equal or 1 hooded and 2 non-hooded tepals; staminodia present, inflexed beneath the maturing ovary. ..... 3. *Pilea.*
  C. Perianth of carpellate flowers either continuous or comprised of 4 mostly fused segments; staminodia absent.
    D. Perianth of carpellate flowers (perfect flowers absent) continuous, tightly covering the mature fruit; style apical and flexed near the tip, stigma linear; plants generally tall, fibrous perennials, stem nonsucculent; stipules or stipule scars present. .... 4. *Boehmeria.*[3]
    D. Perianth of carpellate and perfect flowers accrescent, segments mostly fused; style short or absent, stigma penicillate; plants mostly delicate annuals, stems watery and usually translucent; stipules absent. ..... 5. *Parietaria.*

Tribe Urticeae [Urereae Gaud.]

1. **Urtica** Linnaeus, Sp. Pl. 2: 983. 1753; Gen. Pl. ed. 5. 423. 1754.

Tall, erect or sometimes ascending, fibrous annual or perennial herbs of diverse habitats, including thickets, bottomlands, damp forests, roadsides, shell middens, other waste places, and sometimes fields. Roots in annual species fibrous but usually with a short taproot, or, in perennials, with a horizontal rootstock bearing adventitious roots and aërial branches. Stems generally fluted, mostly hollow, greenish or sometimes purple or red, in certain species bearing numerous stinging hairs on short [or long] pedestals, particularly at nodes. Leaves simple [rarely deeply incised], petiolate, opposite, blade mostly ovate or lanceolate, margins serrate, often with stinging hairs on both upper and lower surfaces; punctiform, rarely linear cystoliths visible on upper surfaces of dried leaves; stipules lanceolate, generally paired at the petiole base, membranaceous, green [or brown], sometimes ciliate, free [or connate], usually persistent. Plants monoecious or dioecious; inflorescences bracteate, basically cymose, flowers organized into lax racemes or aggregated into loose [or tight] clusters that originate from axils of stipules and leaves, in some species zones of stamin-

[3] *Pouzolzia zeylanica* (L.) J. Benn. (tribe Boehmerieae) from Asia, collected once as a weed in Seminole County, Florida, would key out here. For its separation from other members of the family see footnote 5.

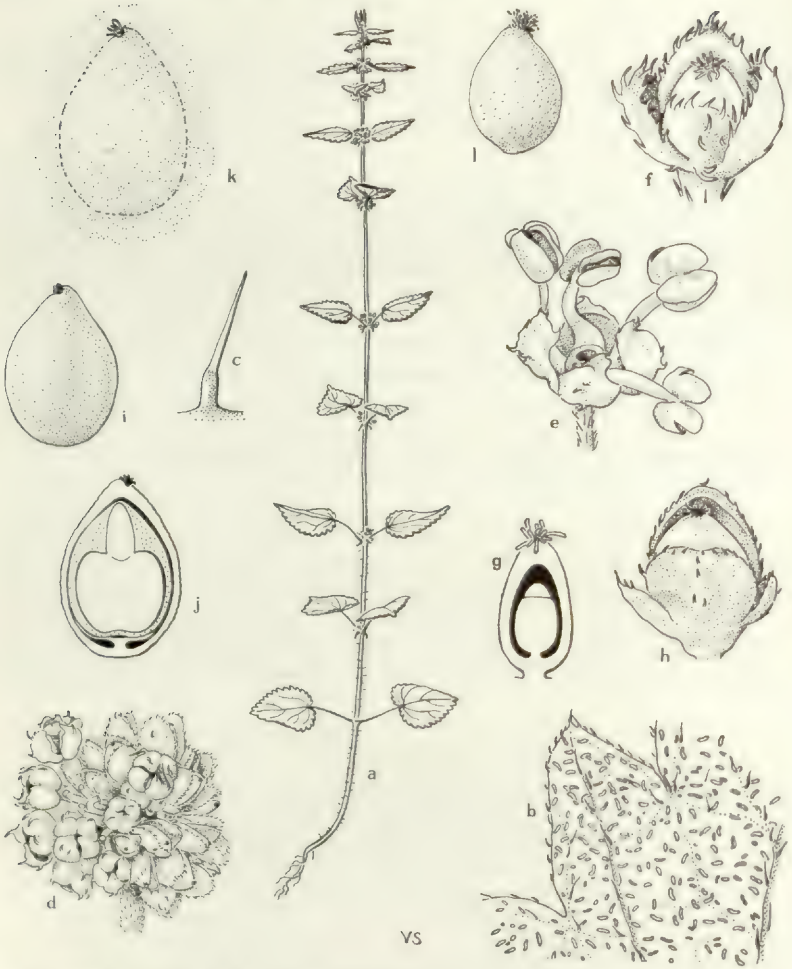

FIGURE 1. **Urtica.** a–k, *U. chamaedryoides*: a, habit of young plant, × ½; b, portion of adaxial leaf surface with cystoliths, × 12; c, stinging hair from petiole, × 12; d, inflorescence with staminate flowers and young fruits, × 6; e, post-anthesin staminate flower, × 12; f, carpellate flower, × 40; g, longitudinal section of ovary with orthotropous ovule, × 50; h, achene and accrescent perianth, × 15; i, mature achene, × 20; j, mature achene in longitudinal section showing embryo, endosperm stippled, × 20; k, wet achene, mucilage halo dotted, × 20. l, *U. dioica*: mature achene, × 20.

ate and carpellate flowers alternating along the axis. Staminate flowers small, pedicellate, greenish or yellowish, with 4 equal, saccate, pubescent tepals sometimes bearing stinging hairs; stamens 4; rudimentary gynoecium small, cuplike. Carpellate flowers minute, subsessile, greenish; tepals 4, decussate, ± equal, pubescent; style absent; stigma apical, central, penicillate; ovule orthotropous, micropyle formed from the inner integu-

ment. Fruit a thin-walled, compressed, ovoid achene, loosely inclosed by enlarged inner tepals, outer tepals remaining small; apical stigmatic tuft persistent or not. Seed coats thin; endosperm fleshy, forming a thin layer around the embryo, some species with a chalazal endosperm haustorium; embryo straight, radicle generally shorter than the ± orbicular, emarginate cotyledons. LECTOTYPE SPECIES: *U. dioica* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 1: 634. 1913. (Classical Latin name, from *urere*, to burn, surely in reference to the stinging hairs.) — NETTLE.

A genus of about 45 species, mostly indigenous to temperate parts of the Northern and Southern Hemispheres, but a few species in the New and Old World tropics, usually in the mountains at middle and upper elevations. *Urtica dioica* L. and *U. urens* L. are exceptionally widespread weeds. In North America *U. gracilis* Ait. extends northward through the Boreal Forest to the edge of the subarctic (also in central Alaska).

The genus is badly in need of monographic study, especially in North America where regional floristic treatments of the perennial species vary dramatically. About 10 species of *Urtica* generally have been recognized on this continent north of Mexico, and of these, seven are perennials. *Urtica californica* Greene, *U. holosericea* Nutt., and *U. Lyallii* S. Wats. occur in western North America; *U. serra* Blume is a species of the Southwest; *U. dioica*, *U. procera* Muhl. ex Willd., and *U. viridis* Rydb. are generally northern and mostly restricted to the central and eastern sections (strictly dioecious plants of *U. dioica* may be entirely introduced from Europe); and *U. gracilis* is northern and transcontinental. *Urtica dioica*, *U. gracilis* (sensu Small, Man. Southeast. Fl. 433. 1933), and *U. procera* (sensu Fernald) have ranges that include a portion of the southeastern United States. The latter two species are often treated as *U. dioica* var. *procera* (Muhl. ex Willd.) Wedd. (Hermann; however, see Hitchcock for a different interpretation). *Urtica dioica* in the broad sense seems clearly to be a circumpolar species complex. The temperate Asian representative of the complex is *U. angustifolia* Fisch. ex Hornem.

Two annual nettles occur in the southeastern United States. The Eurasian *Urtica urens* is sporadically naturalized in Florida, South Carolina, and probably elsewhere in the region. The native *U. chamaedryoides* Pursh, generally a plant of flood plains and rich woods often over limestone, occurs from central Florida west to Texas and Mexico. It is native northward to South Carolina, West Virginia, and Missouri, and occasionally is found as an adventive beyond these states. Disjunct populations have been reported from Argentina. A third annual, *U. gracilenta* Greene, occurs in Arizona, New Mexico, and Texas.

Cystoliths are prominent in the leaves of many *Urtica* species, and both punctate and bacilliform types are present. The effervescence of those in *U. chamaedryoides* and *U. urens* when dilute hydrochloric acid is added indicates that the cystoliths are probably mineralized with calcium carbonate. Specimens of *U. chamaedryoides* generally have bacilliform cystoliths, although a few collections from Texas have been seen with punctiform markings.

Stinging hairs are present or absent on leaves, stems, inflorescence axes, and tepals, and occur on both annual and perennial species. Each hair consists of a single, long, narrow, tapering stinging cell with a sac-like base embedded in a multicellular emergence. The hair is closed at the tip by a small bulb that, when pressure is applied, breaks off along a predetermined line of fracture producing an extremely sharp, bevelled point. Hair cells are reported to be both silicified and calcified. Upon contact with the skin, the hair punctures the surface and compression of the base forces the contained fluid into the wound. Contact with nettles results in a three-phase reaction involving formation of a wheal (associated with itching), reddening, and pain. The chemical basis of these responses has not been fully determined but experimental data obtained from the hairs of *Urtica urens* indicate that in this species histamine and acetylcholine are responsible for the itching and burning sensations, respectively.

Base chromosome numbers for the counted species are $x = 11$, 12, and 13. Diverse chromosome numbers appear to be documented in *Urtica dioica, sensu lato*, $2n = 22$, 52 (*U. kioviensis* Rogowitch = *U. dioica*?), 48, 52 (Löve & Löve), and 52, 76–78 (*U. platyphylla* Wedd. = *U. dioica*?); diploid and tetraploid races occur in *U. urens*, $2n = 24$, 26, and 52. Sex chromosomes tentatively identified in *U. dioica* by Meurman have not been confirmed subsequently (Westergaard).

Little has been written about the dispersal of *Urtica* species. According to Ridley, the achene and perianth (which surrounds the fruit to maturity) may be transported as a unit by passing animals. In some species the stiff, curved, downward-pointing hairs that cover outer tepal surfaces provide the means of attachment. Achenes from the annuals *U. chamaedryoides* and *U. urens* become mucilaginous upon wetting, but those of the perennial nettles *U. dioica*, *U. gracilis*, and *U. procera*, in contrast, do not develop mucilage when placed in water (Miller). Annual and perennial species from other parts of the world should be examined to document this difference further.

The genus is of little importance economically. Young leaves and shoots of *Urtica* species are sometimes made into soup, or, after boiling, are used as a substitute for spinach by the Scots and Irish and in parts of continental Europe. Nettles find similar use in the Canadian Maritime Provinces. In Great Britain, until about 1860, the strong phloem fiber from *U. dioica* was made into cloth. This species was extensively used by the Germans during both World Wars as raw material for certain chemical, food, paper, and textile industries.

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2. **Laportea** Gaudichaud-Beaupré in Freycinet, Voy. Monde Bot. 498. 1830 ('1826'), nom. cons.

Erect, perennial herbs [or shrubs] of moist forests, stream banks, and ravines. Roots tuberous, plants spreading by rhizomes. Aërial branches fluted, covered with stinging hairs. Leaves alternate, petiolate, ovate, serrate [dentate, or shallowly incised], puberulent or not, generally with stinging hairs; cystoliths punctiform (calcium carbonate?), restricted to upper leaf surface; stipules intrapetiolar, bifid toward the apex, fugacious. Plants monoecious; inflorescences axillary, lax bracteate cymose panicles; carpellate and staminate flowers in separate inflorescences [rarely together], the carpellate inflorescences borne higher on the axis than the staminate. Staminate flowers small, greenish, pedicellate [or sessile] with 5 [4] saccate, longitudinally ridged tepals; stamens 5 [4]; rudimentary gynoecium large, obovoid, hyaline. Carpellate flowers small, zygomorphic, borne on a thick pedicel that develops lateral [or dorsi-ventral] wings as the fruit matures; tepals 4, free, the inner pair lateral, green, the outer pair smaller, ciliate, sometimes reddish, the abaxial tepal becoming hood-like and covering part of the pedicel apex; ovary situated on a short disk; style apical, stigma elongate, subulate [sometimes trifid], covered with short hairs; ovule hemi-anatropous, funiculus lengthening during maturation of fruit so that the embryo comes to occupy a horizontal position with respect to the base of the carpel. Fruit a laterally compressed, stipitate achene, partly covered by enlarged lateral tepals, adaxial tepal small,

FIGURE 2. **Laportea.** a–h, *L. canadensis*: a, leaf, adaxial surface, × ¼; b, portion of carpellate inflorescence, cymules containing both flowers (at arrows) and fruits, × 3; c, staminate flower bud, × 30; d, carpellate flower, × 25; e, young fruit in longitudinal section showing position of ovule shortly after fertilization, stigma mostly removed, × 25; f, enlarged perianth with mature achene and winged pedicel, × 10; g, mature achene, × 8; h, mature achene in longitudinal section showing embryo, endosperm white, × 8.

mostly hidden by the mature fruit, abaxial tepal only slightly larger than at anthesis, base of style persistent and displaced laterally by unequal development of the achene and embryo. Seed coats thin; endosperm mealy, sparse; cotyledons large, orbicular, radicle short. (*Urticastrum* Heister ex Fabr., nom. rejic.) LECTOTYPE SPECIES: *L. canadensis* (L.) Wedd.; see Hitchcock & Greene, Prop. Brit. Bot. Int. Bot. Congr. Cambridge, England, 1930. 101. 1929. (Named for François L. de Laporte, a 19th century French entomologist.) — WOOD-NETTLE.

A predominantly Old World genus of 22 species, 12 restricted to either the Malagasy Republic (5 species endemic) or Africa south of the Sahara (Chew, 1969). Other Laporteas occur in Asia (4 species), Polynesia and/or Malesia (2 species), and widely throughout the Old World tropics (1 species). Of those in the Western Hemisphere, *Laportea* (*Fleurya*) *cun-*

eata (A. Rich.) Chew, is known only from Cuba and Hispaniola, *L.* (*Fleurya*) *aestuans* (L.) Chew is widespread in the Caribbean and Central and northern South America (also in the Old World tropics), while *L.* (*Laportea*) *canadensis* (L.) Wedd. is widely distributed in eastern North America from Nova Scotia to southern Manitoba, south to Louisiana and northern Florida. Disjunct stations occur in the eastern Mexican highlands (Nuevo León and Tamaulipas).

Laportea canadensis appears to be most closely related to *L. bulbifera* (Sieb. & Zucc.) Wedd., $2n = 60$, an Asian species ranging from Manchuria, Korea, and Japan, through parts of China to India, the Indochinese Peninsula, Sumatra, and Java (occurring only in the mountains in tropical latitudes). In the southeastern United States, *L. canadensis* is less common on the Coastal Plain and more frequently encountered in the Piedmont and Mountain districts. Typically, it is a species of mesophytic hardwood forests. Although apparently not reported from the United States, *L. aestuans* should be sought in southern peninsular Florida and the Keys.

As presently circumscribed, *Laportea* is composed of sections LAPORTEA (10 species) and FLEURYA (Gaud.) Chew (12 species). Species in sect. LAPORTEA are characterized by symmetrical lateral wings on the fruiting pedicel and by articulated achenes. In members of the sect. FLEURYA, the pedicel wings are asymmetrical and dorsi-ventral in orientation, while the achene remains firmly attached to the pedicel, and the fruit and perianth are dispersed together. Woody species, long placed in *Laportea*, have been segregated as the genus *Dendrocnide* (Miq.) Chew, one member of which, *D. excelsa* (Wedd.) Chew, an endemic of Queensland and New South Wales, Australia, attains a height of 35 m.

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CHEW, W. L. *Laportea* and allied genera (Urticaceae). Gard. Bull. Singapore **21**: 195–208. 1965. [Segregates *Dendrocnide*, unites *Fleurya* and *Laportea*; 23 spp. of *Laportea*, including L. *canadensis*.]

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MACFARLANE, W. V. The stinging properties of *Laportea*. Econ. Bot. **17**: 303–311. 1963. [Irritating fluid from *L. moroides* (= *Dendrocnide moroides*) partially characterized but not identified chemically; not the substances producing the response in *Urtica* spp.]

Tribe ELATOSTEMEAE Gaud. [Procrideae Wedd.]

3. **Pilea** Lindley, Collect. Bot. *ad pl. 4.* 1821, nom. cons.[4]

Erect, ascending, or repent [sometimes scandent or suffrutescent] annual or perennial herbs of rich, moist forests, swampy ground, and weedy habitats. Roots mostly fibrous, but plants often with a short taproot; repent species rooting from nodes. Stems translucent and watery, or fleshy and succulent, or neither. Leaves opposite, equal or anisophyllous; blades ± orbicular, ovate, obovate, or lanceolate, with one strong midvein or triplinerved, margins entire or serrate, glabrous or with sparse, long nonstinging hairs; petioles short or long; cystoliths prominent, linear or fusiform [rarely punctiform], restricted to the adaxial epidermis or occurring in enlarged cells of both the adaxial and abaxial surfaces; stipules intrapetiolar, connate, persistent or not. Plants monoecious [or dioecious]; inflorescences axillary, bracteate, lax or tight compound cymes, carpellate and staminate flowers borne at the same node, but generally on separate branches of the inflorescence. Staminate flowers small, white or sometimes purplish, pedicellate, ± compressed laterally in bud; perianth crowned with short protuberances in bud, the segments initially mostly connate, but separating into 4 (3) tepals at anthesis, segments remaining fused near the base following anthesis; stamens 4 (3); rudimentary gynoecium small, conical. Carpellate flowers with short pedicels, zygomorphic or not; tepals 3, identical, linear, and all slightly expanded at the apex, or, 1 strongly hooded, and 2 identical, lanceolate, and nonhooded; staminodia 3, opposite the tepals, adaxially flexed during fruit maturation and ejecting the fruit from the perianth at maturity; stigma penicillate, mostly falling away after pollination; ovule orthotropous. Fruit a ± symmetrical, laterally compressed, light brown to black achene, surface smooth and mottled, or papillose, or covered with prominent bosses. Endosperm fleshy; cotyledons ovate, not emarginate. (*Adicea* Raf. ex Britton & Brown.[4]) TYPE SPECIES: *Pilea mucosa* Lindl.; see Collect. Bot. *ad pl. 4.* 1821, nom. illeg. = *P. microphylla* (L.) Liebm. (Name from Latin, *pileus*, a felt cap, in reference to the hooded tepal in the type species.) — RICHWEED, CLEARWEED.

A much ignored genus, primarily pantropical, with a few species in temperate parts of the Northern and Southern Hemispheres; absent from Europe, Australia, and New Zealand. *Pilea* is by far the largest genus of the Urticaceae, with over 600 species described, but the actual number probably considerably less than this. The American tropics, especially the Caribbean region, are rich in species. Killip records 112 species from northern and western South America; León & Alain report that of the 64 species occurring in Cuba, 51 are endemic. Four species are found in

[4] Conservation unnecessary because *Adicea* Raf. was not validly published until after 1821 and *Adike* Raf. dates from 1836 (see Taxon 8: 262. 1959). *Adicea* exists as a name only in several of Rafinesque's publications. Britton and Brown (Illus. Fl. No. U. S. 1: 533. 1896) were apparently the first to supply the missing generic description, although several botanists used *Adicea* in the mid-1800's.

eastern North America. The genus is not represented in the western half of this continent.

Weddell's two outdated treatments (1856, 1869; 136 and 159 spp. recognized, respectively), in which *Pilea* is artifically broken down into three sections and a number of lesser categories, mainly on the basis of leaf characteristics, are the only monographs of the entire genus. Killip has recognized 12 informal species-groups based similarly on vegetative traits. Our native species fall into two, perhaps more, natural categories according to the presence or absence of a hooded third tepal.

Section PILEA (*Integrifoliae* Wedd.), containing species with entire leaves, is represented in the Southeast by *Pilea microphylla* (L.) Liebm., artillery plant, $2n = 36$, and *P. herniarioides* (Sw.) Wedd., both restricted to the southern parts of our area but fairly widespread in the American tropics. The former, a plant of pinelands, forests, hammocks, and sometimes weedy places, has been found sporadically throughout Florida (in part escaped from cultivation) and may occur at climatically favorable places elsewhere in the Southeast. It is present in the Old World tropics, probably also as a garden escape, and is grown commonly in greenhouses in temperate regions. *Pilea herniarioides* is known from damp ground and hammocks in southern peninsular Florida and the Keys. It differs from the more fleshy and ascending *P. microphylla* in being repent and in having filiform stems and deltoid to ± orbicular leaves with petioles as long as or longer than the blades (vs. obovate or lanceolate leaves with short petioles). Specimens of *P. herniarioides* from Florida, the West Indies, and South America seem to include several elements, one of which approaches *P. microphylla*. The small, entire-leaved pileas are in need of further study, as a comparison of the descriptions of *P. herniarioides* in Killip (1939, 1960) and Fawcett and Rendle shows. Small (Man. Southeast. Fl. 434. 1933) lists a third member of the section, *P. serpyllifolia* (Poir.) Wedd., from southern Florida and coastal Louisiana, but specimens so-named by Small lack the ciliate leaves characteristic of the type (see Killip, 1939, pp. 479, 480) and appear to be only robust plants of *P. microphylla*.

Species in sect. HETEROPHYLLAE Wedd. have distinctly anisophyllous paired leaves. Both New and Old World members are cited by Weddell (1869), but anisophyllous species of *Pilea* are especially abundant in the American tropics.

Our other two species belong to sect. DENTATAE Wedd., members of which have neither entire nor anisophyllous leaf-pairs. *Pilea pumila* (L.) Gray (including var. *Deamii* (Lunell) Fern.), $2n = 16$, a plant of moist, shaded woods, occurs widely from New Brunswick to North Dakota, south to Texas, Louisiana, Mississippi, Alabama, Georgia, and northern Florida. The less frequently collected *P. fontana* (Lunell) Rydb., in contrast, usually grows in open, swampy or marshy habitats. Although perhaps of wider distribution, literature reports and specimens examined establish its presence from Prince Edward Island westward to North Dakota and south to Nebraska and Indiana in the Midwest, and to the Ridge and

Valley Province of Virginia, and along the Coastal Plain of North and South Carolina, southeastern Georgia, to northeastern Florida in the East. These species are of similar aspect and differ mainly in fruit characters. In *P. fontana* mature achenes (FIGURE 3, o) are black or dark brown, only slightly less broad than long, and often have a narrow, translucent edge and prominent low bosses that do not coincide with a color pattern, should one exist. Fruits of *P. pumila* (FIGURE 3, n) are much narrower, light brown in color, and have a contrasting mottling that appears only slightly raised in relation to the unmottled achene surface.

Pilea has a unique type of fruit dispersal in which the achene is forcefully ejected from the enlarged, but non-adhering, perianth by staminodia. This phenomenon has been investigated in two tropical species, *P. Spruceana* Wedd. (Mosebach) and *P. stipulosa* Miq. (Goebel) and should be studied in our native species as well. For example, the distance the achene is propelled from the parent plant is a critical yet unknown fact in our plants. The mechanism (Mosebach) involves the simultaneous build-up of tension in the three inflexed staminodia, a result both of their anatomy and their being restricted to the confined space beneath the developing fruit. The central cells of the staminodia are larger (to 560 μ long) than the cubical cells of the adaxial epidermis (90 μ) and the longer spindle-shaped abaxial epidermal cells (ca. 275 μ long). When intercell pressure reaches the critical point during the elongation phase of growth, the fruit breaks off the receptacle and is hurled out of the perianth as the staminodia pop outward. (See FIGURE 3, e, k-m.) An adhesive substance produced at the tips of the staminodia apparently helps to hold them under the fruit and prevents their premature extension.

Only a few chromosome counts (9 spp., $2n = 16$, 24, 36, 48, and 52) have been reported for the genus, and, with two exceptions, all for species occurring beyond our region.

At least five species, including *P. Cadierei* Gagnep. & Guillaumin, $2n = 48$, the aluminum plant, are cultivated as ornamentals.

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FIGURE 3. **Pilea.** a–f, *P. microphylla*: a, partially cleared leaf with cystoliths, midvein stippled, × 18; b, axillary staminate and carpellate inflorescences, leaves with inframarginal hydathodes, × 10; c, post-anthesin staminate flower, × 25; d, carpellate flower, × 40; e, nearly mature achene and enlarged perianth (one

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Tribe BOEHMERIEAE Gaud.
Subtribe **Euboehmeriineae** Wedd.

4. **Boehmeria** Jacquin, Enum. Syst. Pl. Ins. Carib. 9. 1760.

Erect, fibrous, perennial herbs [or shrubs to small trees] of swamps, marshes, lake margins, stream banks, and, less frequently, drier situations. Roots fibrous, sometimes thick and fusiform; plants spreading by rhizomes. Stems weakly fluted, glabrous to densely pilose. Leaves decussate or alternate, if decussate, then sometimes alternate on branches, blades broadly ovate to narrowly elliptic, triplinerved, margins serrate or dentate [or shallowly incised], upper surface smooth to strongly scabrous with rigid, forward-pointing hairs, lower surface pilose to white tomentose; cystoliths punctiform, restricted to upper epidermis; stipules lanceolate, brown, usually caducous, and either paired at the petiole base, or intrapetiolar with the apex bifid. Plants monoecious [or dioecious]; inflorescences axillary and bracteate, either ± erect and spicate with carpellate and staminate flowers occurring mixed in remote to congested clusters borne along the main inflorescence axis, the individual staminate flowers surrounded by groups of carpellate flowers within one cluster, or, paniculate

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tepal removed), × 40; f, mature achene, × 40. g–n, *P. pumila*: g, leaf, adaxial surface of blade, × 1; h, axillary infructescence, staminate flowers represented only by pedicels, × 3; i, staminate flower bud in longitudinal section showing inflexed stamens and central, basal, rudimentary gynoecium, × 25; j, carpellate flower and two subtending bracts, × 40; k, nearly mature achene and enlarged perianth, × 15; l, carpellate flower before ejection of achene by staminodia (achene removed), × 15; m, carpellate flower after ejection of achene, × 15; n, mature achene, × 20. o, *P. fontana*: mature achene with bosses on surface, × 20.

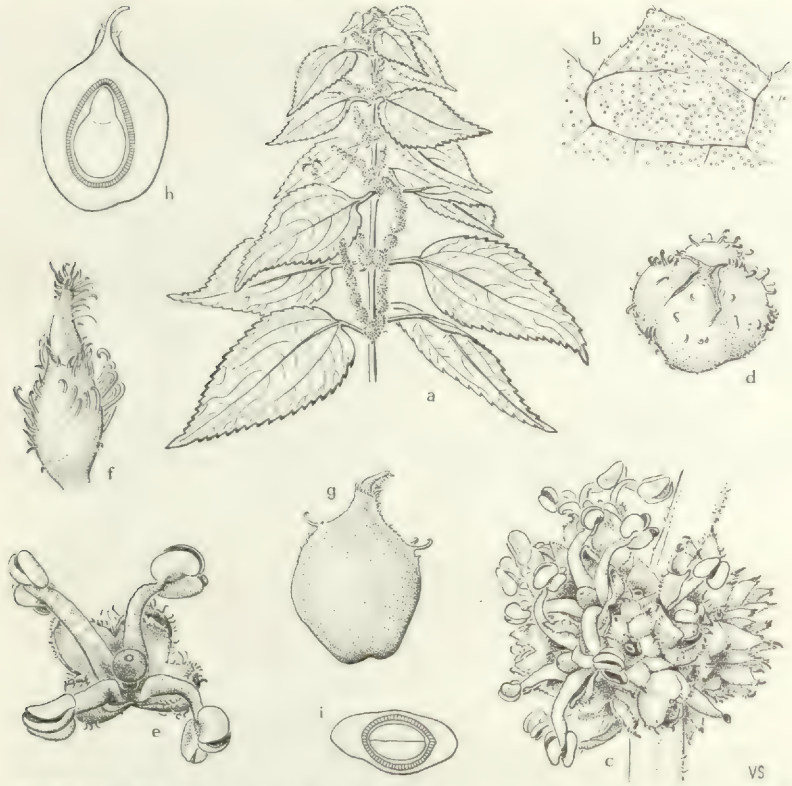

FIGURE 4. **Boehmeria.** a–i, *B. cylindrica*: a, plant apex with axillary inflorescences, × ½; b, cystoliths at edge of adaxial leaf surface, × 10; c, cluster of carpellate and staminate flowers from inflorescence, × 8; d, staminate flower bud showing valvate tepals, × 15; e, post-anthesin staminate flower, × 12; f, carpellate flower, × 40; g, mature fruit covered by persistent perianth, × 20; h, fruit in longitudinal section, endosperm white, endocarp hatched (semidiagrammatic), × 20; i, fruit in cross section, endosperm and endocarp as in *h* (semidiagrammatic), × 20.

and composed of either staminate or carpellate flowers, the staminate inflorescences borne lower on the axis than the carpellate and caducous soon after anthesis. Staminate flowers with short pedicels; tepals 4, valvate, abaxial surfaces bearing numerous hooked and straight hairs; stamens 4; rudimentary gynoecium globose, hyaline to brownish. Carpellate flowers red or brown, sessile; perianth continuous, appressed to the ovary and extending to the base of the style, ciliate or toothed at the apex and bearing hooked or unhooked hairs on the outer surface; ovary stipitate or not; style central, prolonged into a short or long filiform, linear stigma which is flexed near the apex and densely covered along one side with soft trichomes. Fruit either drupaceous and laterally compressed, with the endocarp hard and the outer layers fleshy and thin on two faces but thick

around the edge, or, a ± ovoid, hard-walled achene; in both cases the perianth and withered style persistent [perianth strongly inflated in some]. Endosperm fleshy, sparse; cotyledons ovate, longer than the radicle, not emarginate. (Including *Ramium* Kuntze.) TYPE SPECIES: *B. ramiflora* Jacq.; see Enum. Syst. Pl. Ins. Carib. 31. 1760; Select. Stirp. Am. Hist. 246, 247. *pl. 157*. 1763. (Named in honor of George Rudolph Boehmer, 1723–1803, professor of anatomy and botany at Wittenberg University, Saxony.) — FALSE NETTLE.

A genus of about 100 species, mostly confined to tropical and subtropical latitudes in both New and Old Worlds (poorly represented in Africa), but with species native also to temperate portions of the Northern and Southern Hemispheres; absent from Europe; Australia and New Zealand with one species each. Two species occur in the southeastern United States. *Boehmeria* (subg. TILOCNIDE) *nivea* (L.) Gaud. (*Ramium niveum* (L.) Kuntze), ramie, $2n = 22$, 28, and 42, a native of China, has been widely introduced in the tropics and subtropics as a source of fiber. It has been found as an escape in South Carolina, Florida, and parts of the Gulf Coastal Plain (also near Washington, D. C.), and may be naturalized in some of these areas. The native *B.* (subg. DURETIA) *cylindrica* (L.) Sw., bog-hemp, $2n = 28$, is readily distinguished from ramie by its glabrous to weakly pilose lower leaf surfaces (*vs.* densely white tomentose) and spicate inflorescences (*vs.* paniculate). *Boehmeria cylindrica* (including var. *Drummondiana* (Wedd.) Wedd., and probably *B. decurrens* Small described from specimens collected in northern Florida) ranges from southern Quebec and Ontario west to Minnesota, south to Florida (throughout) and across Nebraska, Kansas, and Oklahoma to Texas. It is known also from southeastern New Mexico and Arizona, Mexico (Coahuila and Tamaulipas to Morelos and Tabasco), Guatemala, Honduras, Costa Rica, Panamá, the Greater Antilles, Bermuda, Trinidad, and as a disjunct in southeastern Brazil, Uruguay, Argentina, and Paraguay.

In North America, *B. cylindrica* is extremely variable in petiole length, leaf blade shape, roughness of upper blade surface, and character of the inflorescence. Forms with rigid, strongly scabrous leaves and short petioles are sometimes separated as var. *Drummondiana*. Although apparently less frequent in the north, it is largely coextensive with var. *cylindrica* but seems to prefer more open habitats. Transplant studies would help to establish whether the variety is merely a sun-form, as has been suggested.

Subgenera were defined by Blume (Mus. Bot. Lugd. Bat. *2*: 194–227. 1857) on the basis of a combination of vegetative, floral, and fruit characters, especially the form of the perianth surrounding the mature fruit. In a treatment of the Asiatic members of subg. DURETIA Blume, Satake proposed seven sections based on shape and pubescence of the perianth. The usefulness of this classification on a world-wide basis remains to be determined by monographic study.

Chromosome numbers for species investigated to date are $2n = 22$, 28, 42, and 52, with 28 and 42 the most frequently reported counts. Okabe

(1963) has found apomixis to be widespread in Japanese species of subg. DURETIA. Sixteen (84 per cent) of the nineteen species he investigated were triploids ($2n = 42$) which, upon embryological study, were found to reproduce through generative apospory. In this type of apomixis the megaspore mother cell does not undergo meiosis, but develops into an embryo sac containing diploid nuclei resulting from mitotic divisions of the mother cell nucleus. The egg cell subsequently gives rise to an embryo without fertilization. Since staminate flowers are rarely produced by most of the investigated species, pollination apparently is not required to stimulate embryo development, in contrast to certain other apomictic plants. The several species studied in subg. TILOCNIDE Blume (including *B. nivea*) were normal, sexually reproducing diploids ($2n = 28$). In Japan, where *Boehmeria* is regarded as a difficult genus, taxonomic treatments have not taken into account the occurrence of apomixis (cf. Satake, who recognized 28 species in subg. DURETIA, many of which are geographically restricted endemics, with Ohwi, who accepts only 10).

Hooked hairs on the outside of the fruiting perianth in *B. cylindrica* probably facilitate dispersal. The fleshy, drupaceous fruits of this species may also be eaten by birds.

The genus is of little economic importance except in China, Formosa, Japan, and the Philippines, where ramie or China grass is grown commercially. Among the several cultivated varieties, *B. nivea* var. *tenacissima* (Roxb.) Miq., rhea, is characterized by sparsely white tomentose to greenish lower surface of the leaves. Propagation is mainly by rhizome cuttings, and varieties high in fiber content have been selected. Ramie is the strongest plant fiber known. Individual fiber cells are exceptionally long (to 5.5 cm. and probably greater, according to Aldaba), and they are reported to absorb water and to dry more quickly than flax. Further, ramie is claimed to be nearly equal to silk in luster and brilliance. But in spite of its many qualities, ramie is not widely utilized because pure fibers are difficult to separate from abundant associated gums. Willimot gives the following uses for ramie: table and household linens, lace, furnishing and bedding textiles, filter cloths, fabric for rubber tires, sewing thread for leather goods, ropes, gas mantles, paper for bank notes, and packing material.

Before the introduction of cotton, ramie was the principal fiber plant in the Far East where its use dates back several millenia. It was introduced into the United States in 1855, but since then, crops have been raised mainly on an experimental basis, mostly at places on the Gulf and southern Atlantic coastal plains and in California. Only a few tons of fiber for commercial use were obtained between 1935 and 1943 from this region. Until better methods of fiber-preparation are devised, high labor costs will keep ramie a minor fiber plant in the United States.

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Tribe PARIETARIEAE Gaud.

5. **Parietaria** Linnaeus, Sp. Pl. 2: 1052. 1753; Gen. Pl. ed. 5. 471. 1754.

Erect, ascending, sometimes decumbent, often multi-stemmed, taprooted annual or perennial herbs [or subshrubs] of moist forests and shaded ground. Stems in annual species translucent, watery, sparsely to densely pubescent with soft, sometimes hooked hairs; stems usually somewhat woody in perennial species. Leaves petiolate, pinnately to ± palmately veined, opposite in seedlings, alternate in mature plants; blades lanceolate, ovate, or deltoid, generally pubescent, margins entire; cystoliths dense, punctiform [rarely otherwise], restricted to the upper leaf epidermis; stipules absent. Plants polygamous; inflorescences few-flowered axillary cymes, one cymule borne on each side of the petiole base, flowers subtended by 1 to 3 green, linear [or deltoid and somewhat foliar], often ciliate [and sometimes basally-fused] bracts, usually bearing cystoliths; basal (first opening) flower in each cymule often bisexual, others generally carpellate; staminate flowers also said to occur, but apparently rare or absent (?) in American species. Carpellate flowers sessile with 4 equal, pubescent tepals, fused toward the base, but free above; ovary short-stipitate or not, attached to a small disklike receptacle; style central, apical or slightly displaced from the ovary tip, short or long, stigma penicillate [or linear]; ovule orthotropous (?), micropyle formed by both integuments. Bisexual flowers apparently proterogynous; tepals 4, equal; stamens 4, anther sacs falling off after anthesis, but filaments persisting inside enlarged perianth; gynoecium as in carpellate flowers. Fruit a shiny, light to dark brown or black, hard-walled, symmetrical or slightly asymmetrical, ovoid achene, with or without a short stipe; style completely caducous or persisting as a small apical or subapical papilla; perianth accrescent and often becoming tubular, dry, brown, of a different shape and size in carpellate and bisexual flowers; achene and perianth apparently dispersed together. Endosperm white, abundant; radicle equal or often longer than the cotyledons. LECTOTYPE SPECIES: *P. officinalis* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 1: 637. 1913. (Name from Latin, *paries*, a wall, the habitat of the species first described.) — PELLITORY.

A genus of about 20 species in two subgenera, occurring mainly within temperate and subtropical latitudes, but occasionally also in the tropics, where often restricted to montane habitats. Subgenus PARIETARIA (subg.

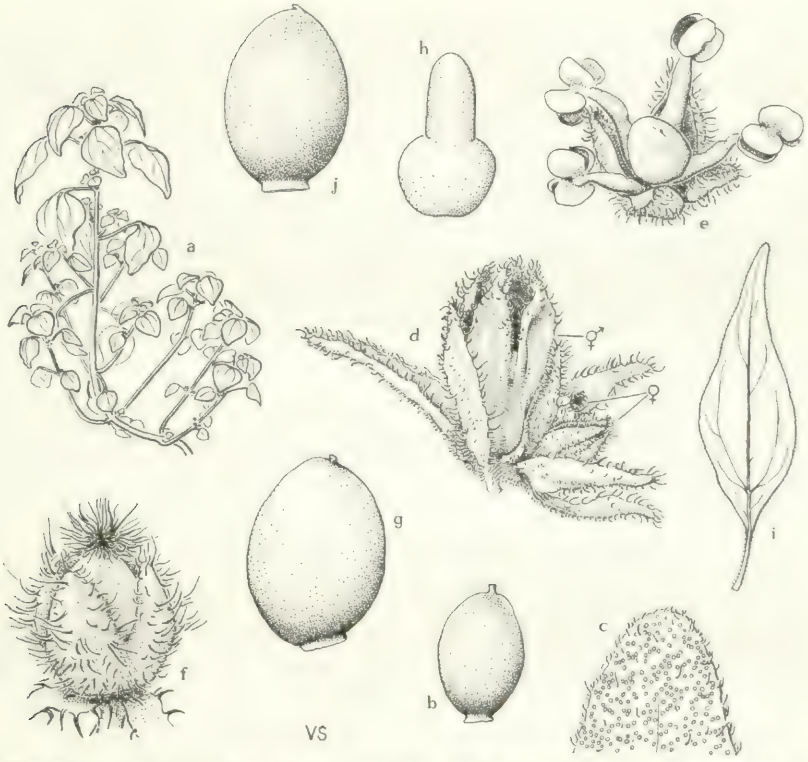

FIGURE 5. **Parietaria.** a, b, *P. floridana*: a, habit of young plant, × ½; b, achene (note flanged stipe), × 25. c–h, *P. praetermissa*: c, adaxial surface of leaf apex with punctiform cystoliths, × 10; d, inflorescence with perfect flower, the perianth accrescent, and two carpellate flowers, × 10; e, perfect flower just after pollen discharge (note absence of stigma, cf. f), × 12; f, carpellate flower, × 25; g, mature achene, × 25; h, embryo, × 25. i, j, *P. pensylvanica*: i, leaf, × 1; j, mature achene, × 25.

Euparietaria Komarov ex Jarmolenko) has long, filiform styles supporting a brush-like stigma, and is comprised mostly of perennials that occur from western Europe and northwestern Africa eastward to central Asia (although *Parietaria macrophylla* Robins. & Greenm., a species of southwestern Mexico, would seem to belong here also). Two members of this subgenus, *P. officinalis* L.[5] and *P. judaica* L., have been infrequently re-

[5] Specimens named *Parietaria officinalis* from Sanford, Seminole County, Florida [shaded places, *Rapp*, April 11, 1929 (NY), sandy, waste places, *Rapp*, July 1929 (NY)] on which Small probably based his statement, "sandy pinelands, old fields, and roadsides, pen. Fla." (Man. Southeast. Fl. 435. 1933), actually represent an apparently unreported adventive in the United States, *Pouzolzia zeylanica* (L.) J. Benn., a native of Asia that ranges from Japan to Formosa, China, Indochina, Malaysia, and India. Although similar in aspect to certain shrubby *Parietaria* species, *Pouzolzia zeylanica* has stipulate leaves and typically a large taproot. Carpellate and staminate flowers subtended by small, scarious bracts are aggregated in tight axillary clusters, and the

ported as adventives at places in the Southeastern United States and elsewhere in North America. Both have black achenes, in contrast to the light to dark brown fruits of our native species. Subgenus FREIREA (Gaud.) Komarov ex Jarmolenko, represented in both the New and Old Worlds, has a sessile stigma or one supported by a very short style. Most species in this subgenus are annuals. The significance of the difference in location of carpellate and bisexual flowers within an inflorescence, used by Jarmolenko (1936) as another distinguishing feature between the two subgenera, needs confirmation.

Three species belonging to subg. FREIREA occur in our region. *Parietaria pensylvanica* Muhl. ex Willd. (including var. *obtusa* (Rydb. ex Small) Shinners), $2n = 16$, occurs widely in North America from southern Maine, Quebec, Manitoba, and British Columbia (not continuously, however), southward to North Carolina, Florida, Alabama, Mississippi, Louisiana, Texas, Mexico, and California. Leaves of this species are typically lanceolate and sparsely pubescent in the eastern United States, where it grows in moist woodlands and other shaded places, but westward plants are generally more hairy, the leaves smaller and often ovate. The ± symmetrical, light brown achenes bearing an apical style remnant are of uniform shape throughout its range, and variation occurs only in size and somewhat in color. *Parietaria floridana* Nutt. (*P. nummularia* Small) and *P. praetermissa* B. D. Hinton (*P. floridana* sensu most authors, not Nutt.[6]) range widely across the Coastal Plain in the Southeast. Occurring in North and South Carolina, Georgia, Florida (throughout), Louisiana, and Missouri, *P. praetermissa* is distinguished by its relatively large (usually longer than 1 mm.), asymmetrically apiculate achenes that lack a flanged stipe. The smaller (usually shorter than 1 mm.), symmetrically apiculate achenes of *P. floridana*, which occurs from Delaware to Florida to Texas, and also in Cuba, are provided with a flanged stipe.

In general species of *Parietaria* are vegetatively polymorphic, and those defined mainly on leaf or bract shape, pubescence, or degree of woodiness may be partly open to reinterpretation (e.g., see Hedberg, who includes the three species described from plants collected in the mountains of East Africa within the range of variation of the widespread *P. debilis* Forst. f.). The most reliable taxonomic characters appear to be shape of the achene and form of the accrescent perianth of both carpellate and bisexual flowers.

Dispersal of certain European species by ants attracted to the achenes by the contents of the basal stipe, which they utilize as a food source, is mentioned by Ridley.

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filiform styles of carpellate flowers drop off soon after anthesis (*vs.* persisting in *Boehmeria*). At maturity, the black, shiny, ovoid achenes (similar to those of *Parietaria officinalis*) are tightly enclosed by a thick, dry, continuous perianth bearing conspicuous ribs. Whether the Sanford plants have persisted, and therefore can be considered naturalized, remains to be determined, as does the status of Small's report of *P. officinalis*.

[6] Treatment of these two species follows Hinton (1968). The type specimens of *P. nummularia* and *P. floridana* represent the same species.

Chromosome counts of $2n = 14$, 16, and 26 have been reported.

The genus is of no economic importance, except possibly for the infrequent use of *P. officinalis* medicinally. Expressed juice and boiled extracts obtained from this species have been used as diuretics and to lower fevers.

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CALLIANDRA HAEMATOCEPHALA: HISTORY, MORPHOLOGY, AND TAXONOMY

Lorin I. Nevling, Jr., and Thomas S. Elias

One of the striking ornamental trees of tropical and subtropical climates is the leguminous powder-puff tree. Since its description more than a century ago it has become a widely distributed ornamental plant. The curious background associated with this species has led to considerable taxonomic and nomenclatural confusion over its correct scientific name. As a result of general interest in the genus *Calliandra*, particularly in its floral biology, we began a routine re-evaluation of *C. haematocephala* Hassk. and *C. inaequilatera* Rusby, the two scientific names commonly associated with the powder-puff tree. Our conclusions differ in several significant respects from those of previous investigators, and we present them in the hope that we have clarified a difficult systematic problem.

One of the most critical problems in equating *Calliandra haematocephala* Hassk. with *Calliandra inaequilatera* Rusby has been that of geographic distribution. *Calliandra haematocephala* was described by Hasskarl from material in cultivation at the botanic garden in Java. In Hasskarl's original publication he cited his material as coming from the botanic garden at Calcutta under the name of "*Ingae haematoxyli*." The origin of the material in Calcutta was reported as unknown. This "species" had not been found in the wild, although it had been widely and correctly assumed to be a plant of American origin.

The type material of *Calliandra inaequilatera* was described by Rusby from material collected by Miguel Bang in Bolivia near the town of Guanai. This locality is also spelled Guanay, Huanai, or Huanay and is apparently critical in the resolution of the problem (see Figure 1). Guanai lies between the fork of the Río Tipuani and the Río Mapiri at an altitude of about 700 meters. It was established by the Spanish as a mission and as a place of exile for political prisoners. At the confluence of the Tipuani and Mapiri the river becomes the Río Kaka, which soon joins the larger Río Beni. One of the difficulties in developing evidence for the conclusion that the two names apply to the same plant has been the failure to resolve the geographic disparity between Bolivia and Java.

It seems unlikely that a Bolivian *Calliandra* would have made its way to Java via Calcutta entirely on its merits as an ornamental shrub by the year 1855 (the date of Hasskarl's publication). We believe that such a "migration" can be explained only through an understanding of the outstanding botanical problem of the times, namely *Cinchona*. The demand for *Cinchona* bark was tremendous at the turn of the 19th century, and field botanists of the era were sending an alarm to their respective governments. Exploitation of the bark of the great *Cinchona* trees was advancing at a much too rapid rate. By 1830 the governments of Britain,

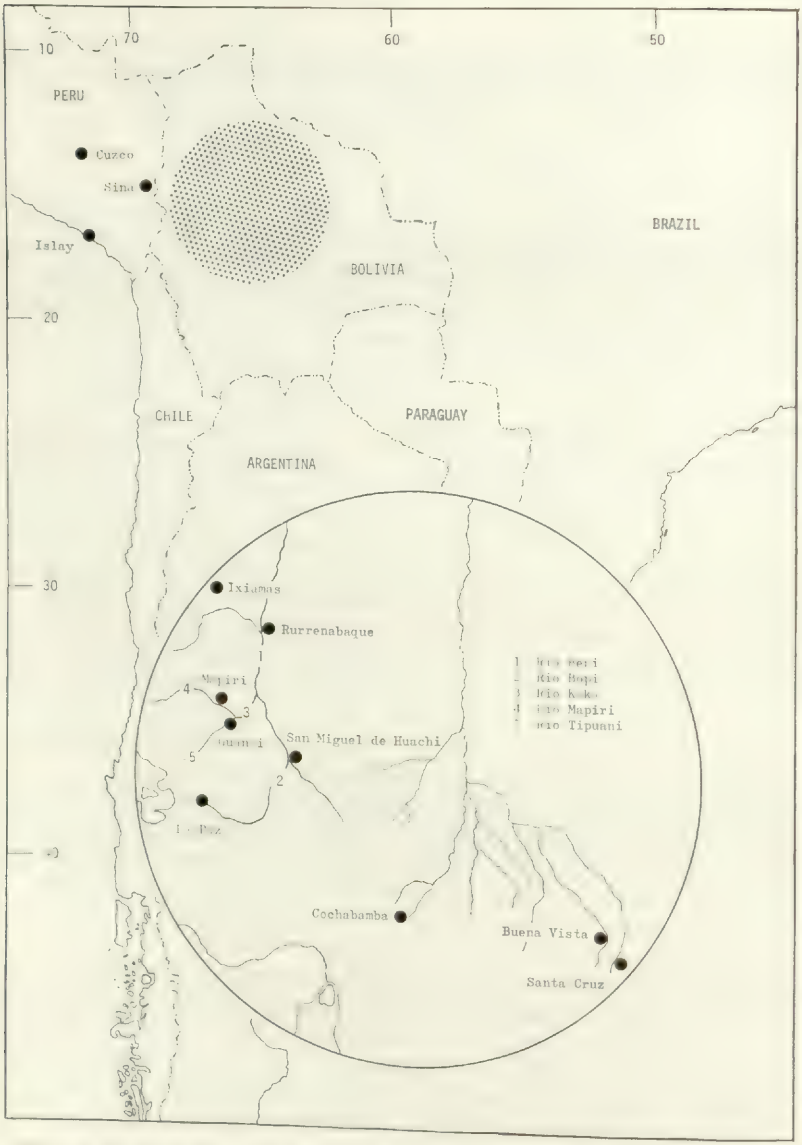

FIGURE 1. Map showing important localities and rivers significant in some historical aspects of *Calliandra haematocephala*. Inset is enlargement of stippled area.

France, and Holland began to believe the field reports and became concerned that their bark source would be dangerously diminished. Testing for high-yielding bark was underway, but it was relatively ineffective because of lack of understanding of the taxonomy of the group. The goal

was to isolate a species that would yield high percentages of sulphate of quinine. At approximately the same time, the Bolivian government realized the threat to her *Cinchona* resources, which were a primary source of income from the outside, and began to take repressive steps to prevent the over-exportation of *Cinchona* bark. In 1845, it granted a five-year monopoly to the Spanish firm of Jorge Tesanos Pinto and Company in return for $119,000. The agreement limited the amount of bark to be taken. In 1849, by presidential decree, the monopoly was broken because of low wages paid to the bark gatherers (*cascarilleros*). Several subsequent monopolies were established, but all collapsed in a few years because of financial difficulties. In spite of the series of impending monopolies, or perhaps because of them, the major powers banded together in various attempts to get seeds or seedling plants of *Cinchona* from various parts of the New World. One of the main objectives was to be *Cinchona calisaya* Wedd. (= *C. officinalis* L. fide Standley). This species was known from southern Peru and Bolivia, but the exact limits of its distribution were unknown. Accordingly, in 1843, the Count de Castelnau, the Viscount d'Osery, and Dr. H. A. Weddell entered Bolivia via an overland route through Brazil to collect material of *Cinchona* and particularly to establish the southern geographical limit of *Cinchona calisaya*. Through a series of mishaps Dr. Weddell was eventually separated from the other members of the party; the Count returned to Europe, while the Viscount disappeared into the upper Amazonian Basin, never to be seen again. Weddell explored the Bolivian *Cinchona* forests from Cochabamba through Ayopaya and Enquisivi. In 1847, he entered the province of Caupolican, went down the Río Tipuani, visited the mission of Guanai (the type locality of *Calliandra inaequilatera*), and then went up the Mapiri. In June of that year, he entered the Peruvian district of Caravaya and went down to Cuzco. Weddell met a Mr. Delondre in Cuzco and, after several days of pleasant but guarded conversation, discovered that he also was searching for *Cinchona calisaya* and, further, that he was a manufacturer of sulphate of quinine. Foreseeing difficulties with the government of Bolivia, Delondre had disassembled a factory for the manufacture of quinine and brought it by ship to the town of Valparaiso where he reassembled it. However, because of the strict limitations put on by the Bolivian government he was unable to obtain bark legally. He had contacted Pinto and Company, but they had sold their total output to a firm in New York for processing.

Weddell and Delondre collected in the valley of Santa Ana. They returned to the coast late in 1847, and Weddell went on to France. In Paris, Weddell's *Cinchona* seed lot was apparently divided, with some seeds being sent to England. The English sent their seeds on to Calcutta for growing, in an attempt to establish a quinine industry in India. After the seeds germinated in Paris the French turned over seedlings to the Dutch who, in turn, sent them directly to Java to start their plantations. The remaining seedlings were sent to Algeria. It seems to us quite possible that Weddell would have collected material other than that of

Cinchona and quite possibly could have collected the *Calliandra* because of its extraordinary beauty and potential use as an ornamental plant. This material could have gone the route from Bolivia to France to England to Calcutta to Java, or from Bolivia to France to Holland to Java. In either case the material could have reached Java, since the botanic garden there was coöperating with the one in Calcutta, and material was exchanged regularly. In addition, part of the Weddell seed collection apparently was turned over to a Parisian horticultural firm, since the Leiden Botanical Garden received a *Cinchona calisaya* via exchange with it in 1851. Seeds of ornamental species may have followed the same route. Leiden sent the *Cinchona* to Java where it arrived in 1852.

In 1849 Weddell published a classification of *Cinchona* based on his field studies. He was, as a result better qualified in 1851 when he returned to South America. In 1852, he entered the Bolivian *Cinchona* area and explored extensively. In the course of his travels he again passed through Guanai (the type locality of *Calliandra inaequilatera*). The results of this second expedition seem hardly to have been reported, but the seed distribution procedure may have been the same as that arranged at the end of the first one.

In 1852, the Dutch Minister of Colonies decided that a *Cinchona* growing area should be established in the colonies. He employed Justus Charles Hasskarl (1811–1894), a botanist who had been an assistant curator of gardens in Java for a period that ended in 1845. After receiving instructions in Holland, Hasskarl sailed from The Hague on December 4, 1852, charged "to collect plants and seeds of as many different species as possible." These instructions referred to species of *Cinchona*, but, since he was formerly associated with a botanic garden, it is unlikely that he would restrict his collecting to a single genus.

The expedition was publicized in a German newspaper, and, fearing that he would be unable to land in South America because of the publicity, Hasskarl sailed with a false passport under the name of José Carlos Müller. He landed in Lima and collected in Peru during the remainder of 1853 and the beginning of 1854. In March, 1854, he crossed the Andes to Puno "and after wandering over part of Bolivia," in April reached the village of Sina in the province of Caravaya near the frontier between Peru and Bolivia. It should be noted, in addition to his having wandered over "part of Bolivia," that Sina is only about 130 miles from Guanai, and it is quite conceivable that material of *Calliandra* could have been collected by him during this period. At this time Hasskarl, as José Carlos Müller, made an illegal purchase of 400 plants of *Cinchona calisaya* through an unscrupulous Bolivian agent. These were collected by a native near Ychu-corpa on the Bolivian frontier.

Once he had the plants, Hasskarl took them to the Peruvian port of Islay, which is just north of the town of Mollendo. He had sent ahead word for help, and the Dutch warship *Prins Frederick Hendrik* met him in Islay. The plants were placed in Wardian cases, and the ship set sail August 27, 1854. It was routed directly to Java and arrived December

13, 1854. It is widely reported that only two *Cinchona* plants survived, but a contradictory report indicates that there were 75. The latter number is probably correct.

On his return to Java Hasskarl was put in charge of the *Cinchona* cultivation project, and in connection with this he received additional Bolivian *Cinchona* seeds from Paris, presumably some of those collected by Weddell in 1852, and seeds of other species were sent from Peru. Seeds collected by Karsten in Colombia were received through the Governor of Curaçao. The significant point is that Hasskarl was indeed in Bolivia and in the general vicinity of the locality for *Calliandra* in 1854. His publication describing the newly cultivated *Calliandra* was in print by the end of the year of 1855. We think that the evidence, although highly circumstantial, indicates that Hasskarl may have collected the plants in Bolivia, have seen them flower aboard ship in Wardian cases, and at that time may have written his very extensive Latin description. This technique, i.e., description aboard ship, was well known to botanists of that era. Alternatively, it is possible that he did indeed obtain his material from Calcutta, and this, in turn, may have been received from the Weddell expeditions; or perhaps Hasskarl wished to cover his tracks in Bolivia and ascribed the plant to Calcutta without receiving seeds from there.

In 1860, the English botanist C. R. Markham was sent to Bolivia to collect additional material of *Cinchona*. He arrived on April 19th near the town of Crucero in the province of Caravaya and met there a Peruvian, Don Manuel Martel. Don Manuel "had a good deal to say, not very complimentary, about the Dutch agent who had come over to obtain Cinchona plants in 1854 for cultivation in Java." The bad feeling generated by Hasskarl affected Markham's expedition, and it was remarkable that he was able to bring his plants and seeds out of Bolivia safely. It should also be mentioned that the Bolivian agent with whom Müller-Hasskarl had dealt was forced to remove himself to another part of the country because of the threats and in fact, acts of physical violence by the local populace. It seems quite possible, then, that the material that was described either on shipboard or from cultivated material in Java was obtained through one of the tortuous routes described.

In postscript it should be mentioned that because of low yields none of the materials collected by these expeditions formed the basis for the rich Java *Cinchona* plantations. The honor of introducing a high-yielding strain fell to Charles Ledger or, perhaps more correctly, to his servant, Manuel Incra Mamani, who collected fourteen pounds of seeds of high-yielding *Cinchona*. One pound was sold to Holland for 100 francs plus £24 on germination. The remaining thirteen pounds of seed were partly sold on the streets of London, and the residue was purchased by a Mr. Money, of India, but on his return to India this lot failed to germinate. After all of the preceding efforts it seems ironical that the profitable Dutch *Cinchona* industry was founded on the purchase of a single pound of seed.

The history of the introduction of *Calliandra inaequilatera* into cultivation is almost as convoluted as that of *Calliandra haematocephala* but fortunately is better documented. Again the geographical focal point is the Bolivian town of Guanai. The first significant botanical event in the history of this *Calliandra* probably was a visit by Dr. H. H. Rusby, Dean of the College of Pharmacy of Columbia University, to Guanai in the course of his expedition of 1885–86. This particular expedition marked the beginning of Rusby's work in Bolivia. At the time he believed that he had arrived in Guanai approximately "three weeks too late," since the forest was primarily in fruit. This seems to be a curious situation, but he wrote that "the forest at that point consists almost wholly of mimoseae in prodigious variety." He said further that "the slope just back of the town was heavily forested, many of the trees being of really gigantic size. They belong chiefly in the senna, mimosa, and laurel families." In spite of the fact that most of the legumes apparently were in fruit, extensive collections were made, but most of these were lost in a boat mishap.

In 1889, Rusby hired Miguel Bang to collect herbarium material for him. Bang had been trained in gardening at Kew and had gone to Bolivia in 1883 expressly to collect living orchids to send to England. The enterprise failed, and Bang began collecting for Rusby. The herbarium material prepared by Bang was offered for sale from New York at $10 per hundred specimens. Eventually this enterprise also failed, and Rusby was forced to suspend employment of Bang. The type material of *Calliandra inaequilatera* was collected by Bang in July, 1892, in the vicinity of Guanai. How large the individual gathering (*Bang 1586*) was, we do not know, except that six specimens have been reunited during this study. Apparently, no morphological information was included with the Bang collections, only a general locality and date. From this collection Rusby described *Calliandra inaequilatera* in 1896. The material was in flower only, and no fruit was seen.

The next important event was the Mulford Expedition for Biological Exploration of the Amazon Basin headed by Rusby (on his final Bolivian expedition). It was organized to make biological collections, field studies, and explorations on the eastern flanks of the Andes in Bolivia, Brazil, and Colombia. "The best equipped expedition ever to leave New York" concentrated early efforts on biological collecting in Bolivia. Among those accompanying Rusby was Dr. O. E. White, plant breeder from the Brooklyn Botanical Garden, who jointly represented the Brooklyn Botanical Garden and the Bussey Institution of Harvard University White, in addition to general collecting, obtained seeds of approximately 200 herbs, shrubs, and trees. The excursion began on June 1, 1921, as the group sailed from New York to Africa, Chile, and from there travelled by railroad to La Paz, Bolivia. From there the party proceeded by mule train and river travel in the general direction of the Amazon drainage. Collections were made along the Río Bopi, which drains into the Río Beni above the confluence of the Río Kaka. They established several

base camps, including ones at Huachi and Rurrenabaque; made extensive collections along the Río Beni, and at Rurrenabaque they had a temporary reunion with Miguel Bang.

We think that it was in the Río Bopi-Río Beni drainage that White collected seeds of *Calliandra*. Indirect evidence (see discussion of chromosome numbers) points to the origin as "Huachi" (San Miguel de Huachi). Because of illness Rusby was forced to leave for New York in December, leaving White in charge of the faltering expedition. White continued collecting until March 15, when the expedition disintegrated, from the biological point of view, and he and some of his companions left for New York, via the Amazon River. Shortly after White's return on April 14, 1922, the dried specimens were sent to Rusby at the New York Botanical Garden, while White took the seeds to the Brooklyn Botanical Garden. Eleven years later the Brooklyn Botanical Garden exhibited a vase of flowering *C. inaequilatera* at the January 20th meeting of the Horticultural Society of New York and won an Award of Merit for the entry. One of the plants from the original seed lot, now a repeatedly pruned tree with a trunk eighteen inches in diameter, is still growing in the Brooklyn collection.

According to Hayward (1955), the first record of the shrub's introduction into Florida was three plants of *Calliandra inaequilatera* that were sent in 1933 to Dr. George Tyrell, a horticulturist at LaBelle, Florida. He, in turn, gave stock to Dr. E. A. Menninger, who is responsible for its wide distribution and status as a desirable ornamental for tropical climates. The primary method of propagation of the plant is by the seed (Menninger, *in litt.*), although the progeny are variable and not reliable. The plants seem to be quite variable in regard to the number of fruits set, and some plants seldom fruit. The principal horticultural selections have been made on the basis of the color of the staminal filaments, the most conspicuous parts of the showy heads of flowers.

Recently (1963), Cowan in reviewing the taxonomy of the cultivated powder-puff trees concluded that two species, *Calliandra haematocephala* and *C. inaequilatera* are being grown. He presented keys, descriptions, and discussion of each species. His maintenance of the two as distinct species was based, not on opposing qualitative characters, but on variations of the same quantitative characters, usually with considerable overlapping. We have carefully re-examined the vegetative characters, including petiole length, terminal leaflet size, and degree of leaflet pubescence, which supposedly were useful in distinguishing the two species. The petioles of *C. haematocephala* were reported to be 10–20(–25) mm. long, while those of *C. inaequilatera* were (15–)25–40(–50) mm. long. In addition, his study indicated that the median and terminal leaflets of *C. haematocephala* are smaller, [20–]23–47 mm. long by [5–]7–17 mm. broad, and more numerous than those of *C. inaequilatera*, which are [45–]50–75 mm. long by [15–]20–30 mm. broad. Our own study shows that petiole length, a highly variable character, is independent of leaflet size

and number, with both short to long petioles being found on specimens attributed to each of the two "species" in question.

Although selected elements of Old World cultivated "populations" of *C. haematocephala* can be separated on the basis of leaflet size from similar selected elements of *C. inaequilatera*, there is complete gradation between the two on this character. Indeed, many specimens have intermediate leaflet sizes. Examination of living plants substantiated the unreliability of this character, for leaves with small leaflets can be found on the same branch with leaves with large leaflets (see FIGURE 2). The Old World specimens typically have the leaves glabrate and ciliolate, whereas New World ones have varying amounts of leaflet pubescence. We suspect that this is due primarily to a more restricted genotype in the Old World material, probably because of a smaller original sample size. An examination of the holotype and five isotypes of *C. inaequilatera* showed considerable variation in the degree of pubescence of the leaflets.

The floral characters, corolla-lobe size and position in age, length of the

FIGURE 2. Outlines of four leaves from a single vegetative branch of *Calliandra haematocephala* showing size variation.

corolla tube, and peduncle length were also examined and found to be unreliable in distinguishing the two "elements." Although a longer peduncle length is usually found in plants with smaller and narrower leaflets, no clear separation could be made, for the peduncular lengths of *Calliandra haematocephala* overlap with those of *C. inaequilatera*. Likewise, the longer lanceolate corolla lobes attributed to *C. haematocephala*, as well as shorter, more ovate ones, could be found on specimens of *C. inaequilatera*. The length of the corolla tube, like the other characters examined, showed a continuous gradation from 3 to 7 mm. The position of the corolla lobes, erect *versus* reflexed, could not be adequately assessed. This condition does not appear to be genetically controlled. Some of the lobes becoming reflexed may result from the pressing techniques of the collector. In sum, the taxonomic characteristics of the flowers, as well as those of the vegetative parts, fail to differentiate two taxa after a careful analysis of a sizable sample of specimens, both wild and cultivated.

The unreliability of the characters previously used to distinguish the two "species" of *Calliandra* is not in itself sufficient reason to treat them as a single species because of the peculiar circumstances that led to the plant's being known to science in cultivation prior to its being known to science in nature. In the following paragraphs we point out a few peculiar morphological features which link the specimens into a single species and when considered in conjunction with the historical aspects serve to confirm further the morphological conclusions. On the totality of these considerations we believe that there is no justification for recognition of more than one species, the correct name of which is *C. haematocephala* Hasskarl.

The most unique floral feature of *Calliandra haematocephala* is the structure of the androecium. As in all species of the genus, the stamens are basally connate into a staminal tube of varying length. In *C. haematocephala* the tube generally equals or exceeds the corolla lobes (see FIGURE 3.) An irregular number of small fimbriae are inserted at the mouth of the staminal tube. These fimbriae, which have been referred to in previous literature as a "quasi corona," are irregular in both size and shape (generally not more than 1 mm. in length) and often erose at their apices. They are derived from staminal tissue at the orifice of the filament tube, and they may either represent aborted stamens or be irregular enations that are not vascularized. The fimbriae are oriented with their apices directed towards the center of the staminal tube orifice and form a somewhat dome-shaped structure covering it in functionally staminate flowers or permitting only the style to pass in bisexual flowers. They are white, as is the staminal tube, in stark contrast to the variously red-hued filaments. That such an abrupt color change occurs at the filament tube orifice implies more than casual biological significance. This significance probably can be determined properly only in field studies.

It has been long recognized that in *Calliandra*, as in many other genera of the Mimosoideae, the pollen is found in "massulae," or clumps. In *Calliandra* two types of "massulae" are found: a sixteen-grained, disc-like polyad

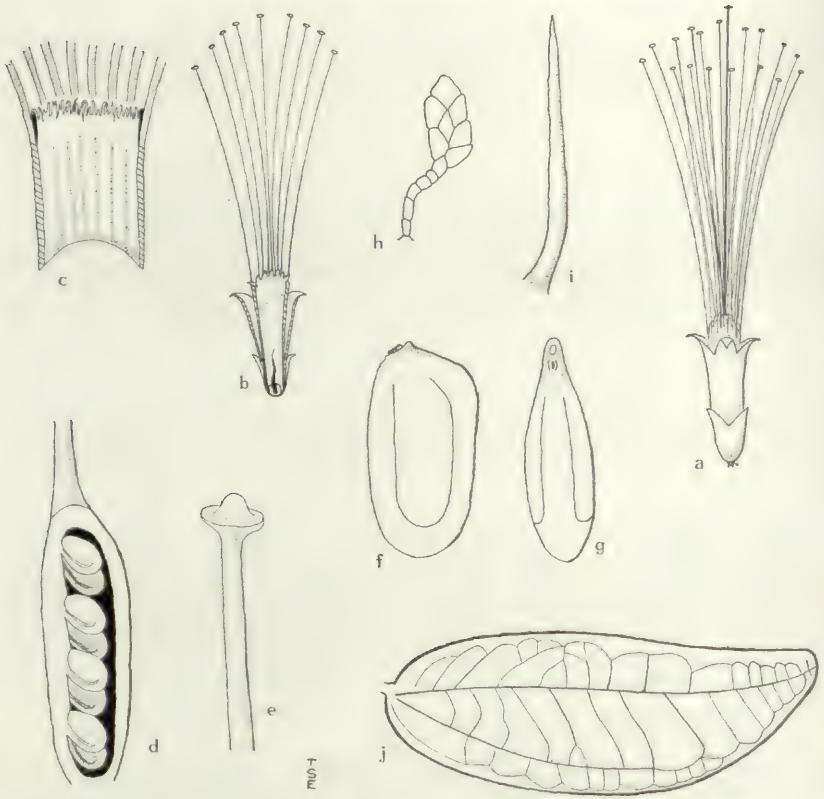

FIGURE 3. *Calliandra haematocephala*: a, bisexual flower, × 1.5; b, longitudinal section of functionally staminate flower, × 1.5; c, longitudinal section and internal view of upper portion of filament tube showing fimbriae, × 5; d, longitudinal section of ovary, × 45; e, portion of upper style and stigma, × 45; f, lateral view of seed showing pronounced U-shaped pleurogram, × 5; g, face view of seed showing pleurogram, micropyle, and hilum, × 5; h, multicellular trichome, × 215; i, unicellular trichome, × 215; j, mature leaflet with prominent venation, × 2.

and an eight-grained, flattened ellipsoidal polyad. The polyad of *C. haematocephala* is of the latter type (FIGURE 4). Although it has been figured in both systematic (Kunth, Mimos. Pl. Légum. 70–73, *t. 22*. 1820) and palynological texts (G. Erdtman, Handbook of Palynology, Munksgaard. 378. 379. 1969) its taxonomic and biological significance has never been realized. The morphology and orientation of the "massulae" is of extreme importance in determining the biological significance of this polyad. In *C. haematocephala* the staminal filaments are erect at anthesis and form the major portion of the so-called "powder puff." The anthers are attached on the back in a median position at right angles to the axis of the filaments. Thus the "face" of the anther is directed away from the center

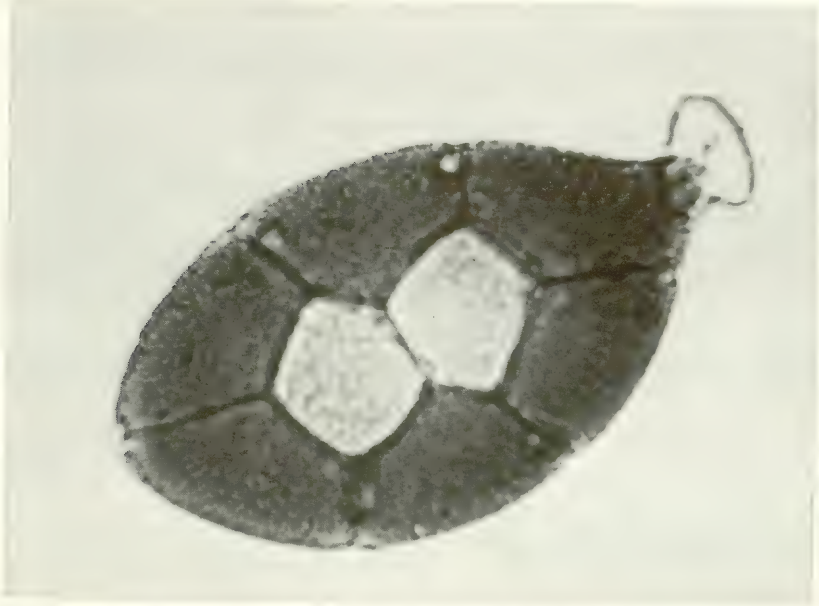

FIGURE 4. Photomicrograph of fresh polyad of *Calliandra haematocephala* stained with aniline blue in lactophenol. The adhesive droplet in upper right-hand quadrat distorted from normal spherical shape because of attachment to microscope slide. Actual length of polyad ca. 160 μ.

of the inflorescence. Flowering proceeds from the base of the inflorescence to the apex but the process is so rapid that, for practical purposes, it may be considered synchronous. As soon as the filament straightens, the anther begins to open by two longitudinal slits. Within each of the four anther locules lie two yellow eight-grained polyads. Each flattened polyad is composed of two median pollen grains and six peripheral ones. One of the peripheral grains is modified slightly and has a somewhat eccentric and pronounced projection. This special grain, the foot grain, lies at the proximal end of each polyad and the two foot grains of the polyad pair are directed toward one another. All previous published illustrations of the eight-grained *Calliandra* polyad show this detail but not the orientation within the anther. The significant point that has not been mentioned is that between the apices of the "foot grains" an extremely viscous substance (that cannot be seen in acetylized material) is formed. As the anther opens the polyads are not only exposed, but the polyad pairs are separated, and their sticky apices are rotated until they are directed away from the anther by at least 90 degrees. The polyad bases are held in the old locules. The mechanism of this maneuver is not known, but it may be related to a rather large disc-like structure on the back of the anther that surrounds the filament. At anthesis the polyads are held with their apices directed outwards, and each apex is covered by a glistening drop of ad-

hesive material. Analogy to the pollinia of Asclepiadaceae and Orchidaceae is irresistible. In an inflorescence of some forty flowers (which seems to be an average number in an inflorescence of a well-grown *C. haematocephala*) there may be approximately 25 anthers per flower (varying between 20 and 30), making approximately 8000 polyads available for pollination. This number coupled with the polyad orientation presents a formidable mechanism for any pollinator to avoid. Unfortunately, we do not know the pollinator, but on the basis of inflorescence position, filament color, and direct observation of other species, one suspects humming birds (and if so, this would account for the restriction of this type of polyad to the New World species of *Calliandra* and would thoroughly substantiate the opinion that the original plants of *C. haematocephala* were of New World origin). The slightest contact with the adhesive drop of the polyad causes the polyad to be transferred to the vector, as can easily be demonstrated in the laboratory with a needle or glass slide. About midway through the first day of anthesis the stigmatic surface is at a level with the anthers and becomes glistening and quite sticky. Polyads touched to the stigma at this time easily break their original attachment and become adherent to the stigmatic surface. By the second day of anthesis the stigma seems to be somewhat less receptive, and stylar elongation has elevated it beyond the horizon of anthers. The wilting of individual flowers begins towards the end of the second day and usually is completed early in the third day.

Individual inflorescences vary in the total number of flowers and in their functional capabilities. The androecium is functional in all flowers, but varying numbers have the gynoecium aborted. The result is that bisexual and functionally staminate flowers are found in most inflorescences, and the ratio of polyads to stigmatic surfaces is therefore greatly increased. In *Calliandra haematocephala* we have found a general tendency for the bisexual flowers to be clustered towards the center of the inflorescence (individual inflorescences thus assuming the functional role in pollination of an individual flower). In a few instances the entire inflorescence was composed of functionally staminate flowers. In other species of *Calliandra* the tendency towards dimorphism is developed to the extent of producing truly dimorphic flowers. A further development in the efficiency of the reproductive cycle is found in the ovary of the bisexual flowers, which has only eight ovules. Thus the transfer and proper germination of a single polyad could assure fertilization of all available ovules. In sum, the reproductive cycle in *Calliandra haematocephala* appears to be highly specialized with a high correlation of ovule number with polyad pollen grain number.

A detailed account of micro- and megasporogensis (lacking any mention of the pollination mechanism) has been presented by Dnyansagar (1958). He concluded that the eight-grained polyad of *Calliandra haematocephala* is composed of two isobilateral tetrads. The individual pollen grains are binucleate according to Dnyansagar but Brewbaker (1967) has reported them to be trinucleate (in *C. inaequilatera*). Most likely one of

these reports is incorrect as a result of misidentification of the specimen.

There are two chromosome number reports for *Calliandra haematocephala*, both made by Earlene Atchison from mitotic divisions. The first count, $2n = 16$, was made from material grown at the Blandy Experimental Farm from Huachi, Bolivia (Jour. Elisha Mitchell Soc. **65**: 118–122. 1949). This count is based on the O. E. White material and provides the only precise information on the origin of the material introduced at Brooklyn. We believe this locality information came directly from Dr. White to Dr. Atchison. The second count, $2n = 16$, was made from material grown at the Atkins Garden, Cuba (Am. Jour. Bot. **38**: 538–546. 1951). An examination of the voucher specimen, *Atchison 91* (GH), shows that it is not *C. haematocephala* but another species of the genus. The only other chromosome count reported for the genus is that for *C. pittieri*, which has $2n = 32$ (Jour. Agri. Sci. Tokyo Nogyo Daigaku **8**: 49–62. 1962).

Calliandra haematocephala Hasskarl, Retzia 1: 216–219. 1855.

Calliandra inaequilatera Rusby, Mem. Torrey Bot. Club **6**: 28, 29. 1896.
Anneslia haematocephala (Hasskarl) Britton & Wilson, Sci. Survey Porto Rico & Virgin Islands **6**: 348. 1926.

Shrubs or small trees to 5 m. high, frequently spreading and forming a ± rounded crown; branches and branchlets terete, the latter with numerous inconspicuous lenticels, glabrate to densely puberulent, with minute multicellular glandular trichomes on most vegetative parts; conspicuous short shoots often present. Leaves alternate, bipinnate, eglandular, with one pair of pinnae, petiolate; petioles canaliculate, 0.7–3.25(–4.75) cm. long, slightly swollen at the base, sparingly puberulent to densely pilose, with a small apiculum between the insertion of the pinnae; rhachides 4.5–11.5(–15) cm. long, canaliculate, sparsely to densely pilose, terminated by a small lanceolate apiculum; pinnae with (4–)5–8(–10) pairs of leaflets; the basal pair of leaflets reduced, subopposite, the inner leaflets smaller, the terminal leaflets narrowly ovate, elliptic, to obovate, 1.5–8.4 cm. long, 0.5–3.5 cm. broad, ± falcate, oblique and rounded at the base, obtuse to acute and mucronulate at the apex, glabrate to pilose, generally ciliolate, with 3 primary veins (2 prominent and 1 subprominent) palmately arranged, chartaceous; stipules ovate to infrequently lanceolate, 2–10 mm. long, 1–3 mm. broad at the base, acute at the apex, persistent, often crowded on the short shoots. Inflorescences capitate, 20–45-flowered, borne singly or in pairs in the leaf axils, pedunculate, the peduncles erect, 1.2–3.3(–5.3) cm. long, pilose, often densely so. Flowers bisexual or functionally staminate by gynoecial abortion, 5-merous, pseudo-actinomorphic, sessile, bracteate, the bracts elliptic, to 1.5 mm. long, striate and ciliolate. Calyx tubular to subcampanulate, 1.5–3 mm. long, striate and sparsely puberulous to glabrate, greenish, the lobes ovate, 0.5–1 mm. long, obtuse at the apex, ciliolate, erect, aestivation valvate. Corolla tubular and flaring slightly towards the orifice, 3.5–8 mm. long, glabrous or with

a few unicellular trichomes interspersed with minute, multicellular, glandular trichomes, reddish, the lobes lanceolate, 2–3 mm. long, ca. 1.5 mm. broad at the base, sparsely ciliolate, usually erect at anthesis, aestivation valvate. Stamens ca. 25, basally connate into a staminal tube, the tube usually equalling or often surpassing the corolla lobes, with numerous irregularly shaped fimbriae, to 1.5 mm. long, inserted within the orifice and forming a dome-like structure at the tube apex, the filaments becoming free at various levels, filiform, 3–4 cm. long, white at base to various intensities of red towards apex; anthers oblong, attached on the back, with a disc-like structure surrounding filament at the point of attachment, dehiscing by longitudinal slits directed away from base of flower; pollen united into 8-grained polyads, the polyads elliptic and flattened, 160 μ long, and ca. 88 μ broad, with one grain eccentric and bearing a drop of adhesive material, each anther bearing 8 polyads. Disc cupuliform, 0.5–0.75 mm. tall, fleshy, glabrous. Gynoecium 1-carpellate, the ovary tetragonal, 3–4 mm. long, glabrous, the style filiform, 3–4 cm. long, red, glabrous, the stigma dome-shaped, ca. 0.5 mm. in diameter, adhesive at anthesis; ovules anatropous, 8; in functionally staminate flowers the aborted gynoecium of various sizes. Legume elastically dehiscent, linear-oblanceolate, 8–12 cm. long, 1–1.5 cm. broad, with a broad valve and narrow but conspicuous margins, brown, usually 5–6-seeded, the seeds oblong, flattened laterally, 0.8–1.2 cm. long, 0.4–0.6 cm. broad, each side marked with a conspicuous pleurogram, hilum eccentric.

SPECIMENS EXAMINED (SPONTANEOUS):

Bolivia. LA PAZ: vicinity of Guanai, July 1892, *Bang 1586* (holotype NY; isotypes A, GH, MO, NY); Ixiamas, Dec. 15, 1921, *Cardenas 2011* (BKL, GH); Isapuri (on Río Kaka) Oct. 5, 1901, *R. S. Williams 725* (K, NY, US). SANTA CRUZ: Buena Vista, April 1–26, 1921, *Steinbach 5612* (A, GH), June 26, 1925, *Steinbach 7154* (A, GH); Santa Cruz, May 1892, *Kuntze s.n.* (US), June 1892, *Kuntze s.n.* (NY), July 2, 1968, *H. Adolfo M.* (US); between Puerto Chuelo and Buena Vista, Mar. 14, 1964, *Badcock 10* (K).

SPECIMENS EXAMINED (CULTIVATED):

United States. CONNECTICUT: Danielson, Logee's Greenhouses, July 1969, *Gibson 1246* (AAH). NEW YORK: Brooklyn Botanic Garden, Mar. 1932, *Everett s.n.* (BH–2 sheets), Mar. 1970, *McGourty* (origin, Bolivia) (AAH), New York Botanical Garden, Nov. 1955 (NY). PENNSYLVANIA: Kennett Square, Longwood Gardens, Dec. 1955, *Huttleston 1203* (AAH, GH, NA), Jan. 1961, *Huttleston 1838* (origin, Edinburgh Bot. Gard.) (AAH, BH), Jan. 1961, *Huttleston 1839* (origin, Florida) (BH), Jan. 1961, *Huttleston 1841* (origin São Paulo, Brazil) (BH), Jan. 1963, *Peele 1008* (origin, Atkins Garden, Cuba) (BH), Jan. 1964, *Peele 1254* (BH), Jan. 1964, *Huttleston 2021* (origin, Atkins Garden, Cuba) (NA). FLORIDA: Fairchild Tropical Garden, Dec. 1959, *Howard 14929* (AAH), Feb. 1969, *Gillis 7582* (NA); Homestead Experiment Station, Feb. 1955, *Sheehan R2* (BH); Naples, Caribbean Gardens, Feb. 1967, *Cooley & Brumbach 11815* (AAH); Oneco, Reasoner Bros. Nursery, Jan. 1932, *T. R. Robinson s.n.* (NA); Oneco, Royal Palm Nurseries, Jan. 1932 (BH), Apr. 1932 (BH); Tampa, Mar. 1956, *Reese 942*

(GH, NA); Winter Haven, Dec. 1964, *Mazzeo 846* (NA), Dec. 1967, *Mazzeo 2419* (NA); Winter Haven, Cypress Gardens, Jan. 1968, *Mazzeo 2468 & 2473* (NA); Winter Park, Lakemont Gardens, Feb. 1956, *Wyndham Hayward* (K). TEXAS: Houston, Dec. 1945, *E. Teas s.n.* (CAS). CALIFORNIA: Azusa, Monrovia Nursery, Nov. 1960, *McClintock s.n.* (CAS); University of California campus, Mar. 1964, *McClintock s.n.* (BH, CAS); La Jolla, garden, Mar. 1956, *McNeill s.n.* (CAS); West Los Angeles, Vavra Estate, Jan. 1959, *Raven, Turner & Whitesel C103* (CAS); Santa Barbara, Harvey Estate, Jan. 1957, *C. Smith s.n.* (CAS); Santa Barbara, Hillside Park, Dec. 1956, *McClintock s.n.* (BH, CAS); Santa Monica, Evans and Reeves Nurseries, Nov. 1942, *McClintock s.n.* (BH).

Bermuda. Paget, Botanical Gardens, Nov. 1963, *Manuel 120* (AAH). **Dominican Republic.** Santiago City, May 1956, *Jimenéz s.n.* (US). **Puerto Rico.** Agricultural Experiment Station, Feb. 1921, *Hume 2146* (NA); Hato Rey, Pennock Garden, Feb. 1967, *Howard 16321* (US), *16339* (AAH); Km. 22 on Route 191 through Luquillo Mts., Jan. 1965, *Wagner 741* (AAH). **Curaçao.** Museum Garden, Dec. 1959, *Fr. M. Arnoldo 2257* (US).

Ecuador. Hda. Angelica, Chobo, Aug. 1921, *Popenoe 1351* (US). **British Guiana.** Georgetown, Botanic Gardens, Feb.-Mar. 1922, *Bailey 566* (BH). **Brazil.** Rio de Janeiro, Jardim Botanico, Dec. 1928, *Ducke 16078* (US); São Paulo, Parque Instituto Agronomico, Apr. 1938, *Santoro 1574* (US).

India. Lucknow, National Botanic Gardens, Dec. 1966, *Sharma 68601* (AAH); Dehra Dun, 1928, *Singh 80* (AAH); Bally gunge, Calcutta, Nov. 1877, *Gamble 5792A* (K). **Singapore.** Botanic Garden, Oct. 1924 (BH), 1929, *Clemens & Clemens 22525* (AAH). **Java.** Buitenzorg, Botanic Garden, *Hasskarl s.n.* (AAH, fragment of type material); 1903 (US), Oct. 1903, *Sargent s.n.* (AAH).

Philippines. LUZON: Los Baños, Feb. 1954, *Steiner 493* (US); College of Agriculture Campus, Nov. 1946, *Sulit* PNH 7022 (AAH), Sept. 1949, *Sulit* PNH 9350 (AAH), Dec. 1949, *Sulit* PNH 12189 (AAH), Mar. 1958, *MacDaniels 21* (BH).

United States. HAWAII: Honolulu, Old Pali Rd., Aug. 1961, *McClintock s.n.* (CAS).

England. Royal Botanic Garden, Kew, Mar. 1959, E.N. 211/45 (origin, Peru) (K), Feb. 1938, E.N. 581/32 (origin, Brooklyn Botanic Garden) (K), Jan. 1966, E.N. 211/45 (K), Jan. 1966, E.N. 342/56 (origin, U.S. Dept. Agriculture) (K). **France.** Les Cèdres, St. Jean, Cap-Ferrat, Jan. 1963, *Marnier-Lapostolle* (K) (white-flowered form).

South Africa. Pretoria, Botanic Gardens, Aug. 1967, *Mills 84* (AAH).

Perhaps the impression has been given that because all the cultivated material known as *Calliandra haematocephala* and *C. inaequilatera* must be considered as a single species (and the name *Calliandra haematocephala* applies) that no taxonomic problems remain. This is not the case as there seems to be greater difficulty in determining the range of variation of the species in the wild than that encountered in collating the cultivated with the wild material. In this connection several populations of *Calliandra* must be considered. The first and the most perplexing, is a population that occurs at Guanai and Mapiri. The Mapiri population is represented by *Rusby 1315* (NY) and the Guanai population represented by *Rusby 1314* (NY) and *Bang 1603* (A, GH). As the basis for his *Calliandra boliviana* Britton used the Rusby collections which were made in May, 1886 and which must have been among the specimens not lost in the river. There is no question that the material above belongs to this complex. The

question is whether or not *C. boliviana* should be a synonym of *C. haematocephala*. The flowers are almost identical with those of *C. haematocephala*, except for a very slight difference in the lobing of the calyx. The leaves have far fewer leaflets, and each individual leaflet is much larger than the leaflets found in the collections of *C. haematocephala*. The problem seems to be whether or not these represent two ecological types, i.e., whether or not they are ecologically separate but geographically sympatric species.

A second population of *Calliandra boliviana* occurs in the basin of the Río Bopi in the department of La Paz. This population is represented by *Krukoff 10220a* (A), *Rusby 654* (BKL, GH), and *White 443* (BKL, GH, K). Unfortunately, none of this material is in flower, so no direct comparisons can be made. The leaves tend to be similar to the Guanai-Mapiri population of *C. boliviana*, except perhaps the even fewer and larger leaflets. *Calliandra boliviana* has been placed in the synonymy of *C. bombycina* Benth., an action that appears to be totally unjustified. *Calliandra bombycina* seems to be restricted to the Río Huallaga drainage in the province of San Martín, Peru. The flowers lack fimbriae at the orifice of the staminal tube.

A very interesting population of *Calliandra haematocephala* grows at the town of Buena Vista in the department of Santa Cruz. This population is typified by somewhat smaller flowers than those of the type material of *Calliandra inaequilatera*, and the staminal tube is exserted only slightly and not several millimeters beyond the corolla lobes as one finds in all the Guanai material. There appear to be two leaf sizes present in these collections, probably on different branches, on one of which the leaflets are medium-sized, and on another of which the leaflets are very much reduced in size. In both cases the leaflets are densely pubescent. Steinbach's notes indicate that the plants occur both in the forest and in the pampas region. It is possible that these plants represent a separate but very closely related species, but we have chosen to treat them as *C. haematocephala*.

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A Arnold Arboretum, Harvard University, Cambridge
AAH Arnold Arboretum, Harvard University, Jamaica Plain
BH Bailey Hortorium, Cornell University, Ithaca
BKL Brooklyn Botanic Garden, Brooklyn
CAS California Academy of Sciences, San Francisco
GH Gray Herbarium, Harvard University, Cambridge
K Royal Botanic Gardens, Kew
MO Missouri Botanical Garden, St. Louis
NA United States National Arboretum, Washington
NY New York Botanical Garden, Bronx
US U.S. National Museum, Smithsonian Institution, Washington

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 14. THE ALGAE OF PICO DEL OESTE [1]

JOHN W. FOERSTER

PUERTO RICO is the most easterly and the smallest of the Greater Antilles. The Sierra de Luquillo highlands are located in the northeastern interior. The study site, described in ecological detail by Howard (1968), called Pico del Oeste, is located in these highlands. This peak, 1050 meters above mean sea level, has a vegetational veneer referred to as an elfin forest (Howard, 1968). Gleason and Cook (1927) have also termed this area of windswept ridges above the 700 meter elevation the mossy or elfin forest. Pico del Oeste extending above the 700 meter line into the clouds is exposed to the constant effects of the northeast trade winds which carry moisture-laden clouds up the easterly slopes of the Sierra and keep the forest constantly humid (Liboy & Sabio, 1966; Baynton, 1968, 1969). This high moisture content, coupled to an annual temperature range of 10°C. to 32°C. (average 21°C.) provides conditions adequate for the growth of the regional flora. Baynton (1969) has described the rainfall pattern on the peak as a function of convective, orographic, and synoptic scale weather conditions. He further stated that due to extensive cloud cover the solar radiation is reduced 40 percent. In the two papers by Baynton (1968, 1969) the weather conditions and influences within the study area have been adequately described.

Puerto Rico is an island where numerous phycological studies have been completed. Such workers as Möbius (1888), Wille (1915), Gardner (1927, 1932), Tiffany (1936), Tiffany and Britton (1944), Almodovar (1963), and Halicki (1964) have compiled information concerning freshwater and terrestrial species from the lowland and rain-forest regions of the island. Almodovar (1963) presented a well-documented analysis of the taxonomic history of the Cyanophyta on the island. The remaining algal Divisions have been treated only slightly. As for the algal investigations of the elfin forest, only Liboy and Sabio (1966) have reported on the algal epiphytes. Their work consisted mainly of investigating gelatinous growths on tree trunks, and their casual observations correlate well with this study.

Algae in the tropics have had limited study from an ecological stand-

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point. A study of the algal flora of elevated elfin-like forest regions from around the world, as well as in the Caribbean area, has not been made. Most tropical investigations are carried out at lower elevations and are usually concerned with the aquatic habitat. Other Caribbean islands have been studied taxonomically by West and West (1894, 1899) and Drouet (1942). Taylor (1935) studied the alpine regions of Colombia, but his investigations concerned various lakes which were far above the elevation of the elfin habitat and away from the influence of the northeast trades. Fritsch (1907) noted the extensive subaërial algal flora in the tropics. He reported that Cyanophyta predominate, and Chlorophyta are reduced in numbers, with the green alga *Trentepohlia* being the most successful of the group. No reference was made to subaërial diatoms or flagellates.

The investigation reported here contributes to our knowledge of algae from a tropical area. After completing identification of a series of samples it was noted that the algal flora of the region was not uniformly distributed, but divided into intergrading phyco-synusia. Data are presented to show the epiphytic algal taxa of several habitats including four endemic vascular species, vascular and non-vascular epiphytes, and various ground locations. Further, data are offered to demonstrate gross ecological influences on spatial distribution.

METHODS

Terrestrial algal epiphytes were collected during the months of February, March, April, May, and August 1966, and during February 1968 from the elfin forest on Pico del Oeste, Sierra de Luquillo, Puerto Rico. Each sample was preserved for later analyses and unpreserved co-samples were used to prepare cultures. Specimens were identified and cross referenced, utilizing the present, most up-to-date and available monographic works. The nomenclature adopted is as follows: for the Cyanophyta, Desikachary (1959); for Bacillariophyta, Patrick and Reimer (1966); for the Chlorophyta, Prescott (1962), Randhawa (1959), Saxena (1962), and Islam (1963); for the Chrysophyta, Pyrrophyta, and Euglenophyta, Prescott (1962). Some of the other works employed included Tilden (1910), Drouet and Daily (1956), Van Huerck (1896), Tiffany and Britton (1952), and many other short papers on individual species and genera. Vascular plants were identified by Dr. R. A. Howard of the Arnold Arboretum, Harvard University.

Analyses were made of the probability that numbers of species collected from each location may exhibit preference of substrate, and/or of microclimate. Analysis of variance (ANOVA) was applied to the difference in numbers of algal species found on the various plants and to the difference in number found on the vascular stem at various heights above the ground. Linear regression was further employed to test the height-species number variation and relationship. These gross ecological parameters were chosen as representative of multiple factors, such as light, moisture,

nutrients, etc., which this portion of the study was not equipped to measure directly.

RESULTS AND DISCUSSION

One of the principal realizations conveyed by the data is that species of subaërial algal epiphytes are not uniformly distributed but are segregated into various intergrading phyco-synusia. In this study microhabitation is to be analyzed and related to the physical aspects of vascular host differentiation, height above the ground, and meteorological conditions only. Lyford (1969) has reported that in an area-to-area comparison the trunks of the trees are covered with organic material in an amount that approximates that on the surface of the soil. This would then indicate a somewhat uniform substrate throughout the study site. If this is true, then light, moisture, and temperature become more important limiting factors.

In all samplings the effect of moisture both as wetness and as a light shield appears to be a significant limiting factor. Due to the island's geographical location the seasonal differences in solar radiation are small and only the thickness of the cloud cover would significantly influence the levels of incident light intensity. When the sun is most direct the atmospheric moisture content is greatest, and when its zenith is lowest for the year the atmospheric moisture content is less. The action of moisture as a filter for the light tends to maintain relatively constant light quantities. In fact Baynton (1968) shows monthly mean light intensity to vary from a low of 212 Langleys per square centimeter to a high of 322 Langleys per square centimeter over the year 1966. Though Baynton (1968) has also shown light attenuation to be 40 percent, Szeicz (1966) has reported no loss of spectral components by the light passing through fog.

TABLE 6 is a compilation of the species identified from the February-March 1966 collections. These are related to the vascular host and to their position on the host. Note the high proportion of Cyanophyta which dominate the microhabitats studied. Diatoms were also present.

Lund (1945) and Fritsch (1922) reported diatoms in the terrestrial habitat. They further stated that the amount of moisture appears to be a limiting factor. Liquid moisture in the elfin forest seems to be adequate for diatom growth. Further, the presence of flagellates in the samples was noted. A film of moisture was present in the area where they were found. Baynton (1969) reports that 21.4 percent of the rain falling on the forest canopy flows down the trunks of the vascular hosts. A build-up of moisture near the base of the trunk would then increase the probability of occurrence of species such as diatoms and flagellates which are more susceptible to desiccation than many of the other algae reported. Therefore, the moisture laden winds become extremely important in maintaining an appropriately moist habitat. They also are probably important in providing some of the algal colonizers.

Schlichting (1960, 1961, 1964), along with many others cited by him, has shown that air currents and birds can transport diatoms and flagellates, as well as species from all algal classes. Therefore, in the situation under study the existence of these species in a vegetative state is a distinct possibility as the northeast trade winds carry their moisture-laden air up the mountain slopes. Here the adiabatic cooling condenses the water vapor producing precipitation in the form of rain, clouds, dew, mist, and fog, establishing an environment suitable for algal epiphytes. The precipitation would deposit any of the airborne algae which were trapped as nuclei of condensation during evaporation at lower levels. Further, the migration of temperate zone birds and the wanderings of native bird and other animal species must not be ruled out as a possible source of algal introduction.

TABLE 1 depicts the principle phyco-synusia encountered in the February-March, 1966, collections relating them to the vascular host and

TABLE 1. **Subaërial Epiphytic Phyco-synusia of Four Vascular Species Sampled during February-March, 1966**

VASCULAR HOST	APPEARANCE	MAJOR PHYCO-SYNUSIA	DISTANCE ABOVE GROUND (METERS) 0–1	1–2
Cyathea pubescens	white globular mass	a diatom-filamentous bluegreen association in an extensive Ascomycete fungal mat	X	
Miconia pachyphylla	always moist gelatinous flat mass, greenish-gray	*Stigonema-Lyngbya-Hapalosiphon* (chiefly *Stigonema informe*)		X
Ocotea spathulata	green material on dead leaves	almost pure association of *Hapalosiphon luteolus*	X	
	white, globular gelatinous mass	*Mougeotia caimani* chief species	X	
	green, gelatinous growth	*Hapalosiphon-Trentepohlia*		X
Tabebuia rigida	flat-green gelatinous	*Stigonema-Hapalosiphon-Oedogonium* (*Stigonema* is principle)	X	
	solid mass	*Stigonema-Hapalosiphon-Scytonema* (*Stigonema panniforme* principle)	X	
	flat mass	*Chroococcus-Cylindrocystis-Synechococcus*	X	
	flat mass	*Synechococcus-Cylindrocystis-Frustulia*	X	
	gelatinous, white colony	*Chroococcus-Hapalosiphon-Trentepohlia*		X

their relative height above the ground. It is interesting to note that dominant species change with height on the tree. Particularly, this is noted on *Tabebuia rigida* as the dominance shifts from a *Stigonema* association to a *Trentepohlia* association (a shift from a blue-green to a green algal synusium). The reason for the shift in association dominance, and the diminishing number of species present undoubtedly rests in the microhabitat itself. It is not the purpose of this paper to analyze these various limiting factors, but to point out the composition of the subaërial algal epiphytic flora on the principle vascular plant hosts, and to note the intricacies of the spatial distribution of component species. What causes the variation is still uncertain but physical data indicate that moisture as wetness or as a light shield may be a principal factor. Grubb and Whitmore (1966) report that fog is an important limiting factor in tropical montane forests. For the algae this suggests not only a high atmospheric moisture content, but also light attenuation.

TABLE 2 is a representation of the mean climatic conditions of the sample site for February-March, 1966. The mean temperature is moderate, solar

TABLE 2. Mean Climatic Data for the February-March Period of Sampling *

MEASUREMENT	MEAN READING
Temperature	18.3°C.
Minimum Relative Humidity	80.6%
Langleys (gram calories/cm.^{2})	283.45 (above canopy)
Daily Precipitation	
above canopy	12.7 mm.
below canopy	9.7 mm.
Percent of Time Humidity	
less than 100% above canopy	28.4%
Humidity at ground level	
below canopy	100%

* Means computed from data supplied by Dr. R. A. Howard.

energy is available, precipitation is adequate, and the relative humidity seldom drops below 100 per cent above the forest canopy and appears to remain saturated beneath the forest canopy at ground level.

As previously noted (TABLES 1 and 6) fewer species are found in the February-March samples taken higher up the trunk of the vascular host. Analysis of variance (ANOVA) was applied to test the variation between the samples collected 1 meter above the ground and 2 meters above the ground on *Tabebuia rigida* and *Ocotea spathulata*. A second ANOVA tested the variation between the vascular hosts *Miconia pachyphylla*, *T. rigida* and *O. spathulata*. A third ANOVA tested the variation between *T. rigida*, *O. spathulata* and *Cyathea pubescens*. The hypothesis tested was that there is no difference between mean numbers of species in the samples (H: $\mu_1 = \mu_k$). All results demonstrated that the populations varied signifi-

cantly and the hypothesis was rejected at the 99 per cent level of confidence. A definite variation appears to exist between the samples.

However, it must be pointed out that, while samples were randomly collected, the number of samples on which the statistics are based is of necessity small. The ideas of microhabitat are introduced to demonstrate that the algal flora of the cloud forest is not a superficial veneer, but, as in an aquatic habitat, is distributed in relation to the stress of the microclimate in which it exists. Varying the microclimate may in some instances accentuate or retard various species and thus shift the community structure both quantitatively and qualitatively.

A regression analysis was performed on the height above the ground where samples were collected (X) and the relation of this height to the number of species found (Y). Samples 9 and 10 (see TABLE 6) are not used in this computation because they are isolated growths not found on the trunks of the trees. Though the data are limited, a definite relationship appears to exist and is presented here to demonstrate the possibility of microhabitat existence. The regression equation ($\hat{Y} = 45.5 - 18.2X$) was computed to test the height factor hypothesis, and the line derived (FIGURE 1) showed that as samples were taken higher on the tree trunks the number of species diminished. This is an indirect relationship further qualified by the correlation coefficient ($r = -.757$), a high negative correlation.

Other samplings reported here were made during April-May, 1966, August, 1966, and February, 1968. TABLE 3 is a listing of the algal species from five habitats not previously described. Specimens from a flowing stream (1), from bryophytic ground-covering adjacent to the access road (2), from cement drains at the experimental site on the access road (3), from bryophytic ground-covering receiving some ground water run-off (4), and from a horizontal trunk of *Tabebuia rigida* (5). Again the results of the qualitative survey indicate the existence of microhabitats. The major phyco-synusia are listed in TABLE 4.

It is interesting to note that the diatom *Frustulia rhomboides* var. *capitata* is the most prevalent species in the habitats listed for April-May, 1966. Further, it is thought that this species exhibited polymorphism in the samples investigated. In all samples studied a small number of *F. rhomboides* var. *viridula* were found, a larger number of *F. rhomboides* var. *saxonica*, and an extremely large number of *F. rhomboides* var. *capitata*. In light of Stoermer's recent report (1967) on polymorphism in *Mastogloia*, the probability exists that these three varieties are growth forms, each variety being reduced in size by approximately half in the following order: var. *viridula*, var. *saxonica*, var. *capitata*. Culturing *Frustulia* was not successful, and therefore only field observations can be offered as evidence.

The April-May, 1966, collections were composed mainly of diatoms (1, 2,3,4). The habitats from which the samplings were made were on the ground and bathed in moisture. Specimens from *Tabebuia rigida* were dominated by the blue-green alga *Hapalosiphon*, with many lesser impor-

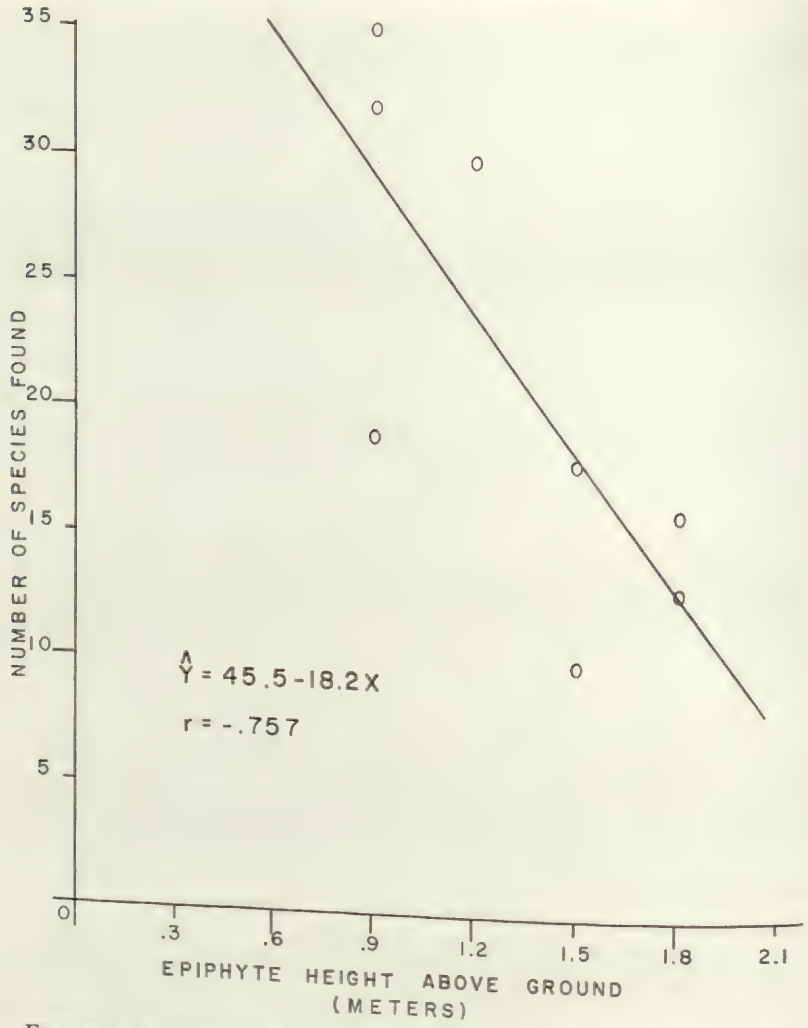

FIGURE 1. Relationship of the height of collection on the vascular host to the number of species from the February-March, 1966 sampling.

tant diatom species. The horizontal trunk of *T. rigida* was approximately one-half meter above the ground under the canopy where light and moisture conditions appear different from the other four sample points.

During August, 1966, approximately the same collection sites that were sampled during February-March were resampled. TABLE 7 is a listing of the species found in relation to the vascular hosts. TABLE 5 is a comparison of major organisms in the various synusia, number of species, and height of collection. A shift from an association dominated by Cyanophyta to one with increased dominance of the Bacillariophyta is indi-

TABLE 3. Species Found in Five Samples Collected during April-May, 1966

SPECIES	HABITAT *
CYANOPHYTA	
Nostocales	
Anabaena sp.	(3) (4)
Aulosira fritschii Bharadw.	(3) (4)
A. prolifica Bharadw.	(4)
Oscillatoria foreaui Frémy	(2)
Stigonematales	
Hapalosiphon welwitschii W. & G. West	(5)
CHLOROPHYTA	
Ulotrichales	
Stichococcus subtilis (Kütz.) Klercker	(1) (2)
Ulothrix variabilis Kütz.	(1) (2)
Zygnematales	
Euastrum sp.	(1) (2)
Cosmarium sp.	(1) (2)
CHRYSOPHYTA	
Rhizochrysidales	
Chrysidiastrum catenatum Lauterb.	(1) (2)
BACILLARIOPHYTA	
Centrales	
Biddulphia favus (Ehrenb.) Van Heurck	(1) (2) (3) (4) (5)
Cyclotella glomerata Bachm.	(5)
Melosira varians C. Ag.	(1) (2)
Pennales	
Achanthes hauckiana Grun.	(5)
A. microcephala (Kütz.) Grun.	(1) (2)
Diatoma vulgare Bory	(1) (2) (5)
Eunotia naegelii Migula	(4)
E. praerupta Ehrenb.	(1)
E. tenella (Grun.) Hust.	(1) (4?) (5)
E. sp.	(4)
Frustulia rhomboides var. *capitata* (A. Mayer) Patr.	(1) (2) (3) (4) (5)
F. rhomboides var. *saxonica* (Rabenh.) DeToni	(1) (2) (3) (4) (5)
F. rhomboides var. *viridula* (Bréb.) Cl.	(1) (2) (3) (4)
Navicula tenelloides Hust.	(1) (2) (4) (5)
N. sp.	(4)
Nitzschia biacrula (?) Hohn & Hellerman	(1) (2)
N. hantzschiana Rabenh.	(5)
Pinnularia sudetica Hilse	(1) (2)
P. viridis var. *minor* Cleve	(4)
Rhopalodia gibberula (Ehrenb.) Mueller	(1) (2) (5)
R. ventricosa (Kütz.) Mueller	(2)

* Sample numbers correspond to the following:
(1) Specimens found growing one inch deep in the water of a flowing stream.
(2) From bryophytic growth covering ground adjacent to access road.
(3) From cement drains along access road.
(4) From bryophytic ground-covering kept wet by rain and clouds, as well as some water flow.
(5) From a growth on a horizontal trunk of *Tabebuia rigida* (two feet off ground).

TABLE 4. **Phyco-synusia of Samples from April-May, 1966**

HABITAT *	SYNUSIA	TOTAL NO. SPECIES
1. In small flowing stream	*Ulothrix-Frustulia*	18
2. On bryophytes near road	*Oscillatoria-Frustulia*	18
3. From cement drains	*Aulosira-Frustulia*	6
4. On bryophytes receiving water run-off	*Aulosira-Frustulia*	13
5. On horizontal trunk of *Tabebuia rigida*	*Hapalosiphon-Frustulia-Trentepohlia*	11

* See also footnote to Table 3.

TABLE 5. **Phyco-synusia of Samples from August, 1966**

HABITAT (vascular host)	SYNUSIA	DISTANCE ABOVE GROUND (METERS) 0–1	1–2	NUMBER OF SPECIES
Tabebuia rigida	*Stigonema-Chroococcus*	X		14
T. rigida	*Aulosira-Zygnemopsis*	X		8
Ocotea spathulata	*Hapalosiphon-Phormidium*	X		13
O. spathulata	*Stigonema-Frustulia*	X		8
Miconia pachyphylla	*Stigonema-Chroococcus*		X	14
Cyathea pubescens	*Navicula-Frustulia*	X		3
T. rigida	*Phormidium-Frustulia*	X		8
T. rigida	*Stigonema-Frustulia*		X	15
O. spathulata	*Aulosira-Frustulia*		X	14

cated. The samplings for February-March, 1966, were made during a period of less rainfall and less cloud cover, and the samplings of August, 1966, were taken during a higher moisture period (Baynton 1968). Baynton (1968) reports longer periods of cloud cover during the month of August. This is the greatest overall comparative meteorological fluctuation on the peak between the two samplings.

A regression analysis was again performed to test the same relationship as discussed for the February-March samples. The line derived (FIGURE 2) by the regression equation ($\hat{Y} = 6.30 + 4.55X$) showed that a positive relationship now exists. This is further qualified by the positive correlation coefficient ($r = .548$). As the samples were taken higher the number of species increased. Since the samples were collected from the same site, and since only a slight change in precipitation, humidity, and temperature was reported (Baynton 1968), it would appear that cloud cover may be an important limiting factor. Though solar radiation has increased, so has the clouding, a factor not as prevalent in the February-March samplings.

TABLE 6. Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966

SPECIES	1	2	*Tabebuia rigida* 6	7	8	3	*Ocotea spathulata* 4	9	*Miconia pachyphylla* 5	*Cyathea pubescens* 10
CYANOPHYTA										
Chroococcales										
Aphanocapsa										
biformis A. Br.					X					
roeseana DeBary	X									
Aphanothece										
clathrata W. & G. West							X			
microscopica Näg.						X				
saxicola Näg.									X	
Chroococcus										
dispersus (Keissler) Lemm.		X		X	X					
dispersus var. *minor* G. M. Sm.	X			X			X			
giganteus W. West			X							
limneticus Lemm.	X									
minor (Kütz.) Näg.				X	X		X			
minutus (Kütz.) Näg.		X	X	X				X		
pallidus Näg.		X		X						
turgidus (Kütz.) Näg.		X	X		X				X	X
varius A. Br.				X					X	
Dactylococcopsis										
smithii R. & F. Chodat							X			
Gloeocapsa										
aeruginosa (Carm.) Kütz.				X						
polydermatica Kütz.								X		
Gloeothece										
linearis var. *composita* G. M. Sm.		X								
Merismopedia										
aeruginea Bréb. ex Kütz.		X								
elegans A. Br. ex Kütz.				X						
glauca (Ehrenb.) Näg.		X		X						
punctata Meyen			X	X						
tenuissima Lemm.				X						
Microcystis										
elabens (Bréb.) Kütz.			X							
incerta Lemm.								X		
Pelogloea										
bacillifera Lauterborn				X						
Rhabdoderma sp.							X			
Synechococcus										
aeruginosus Näg.		X		X	X			X		
Chamaesiphonales										
Chamaesiphon										
confervicola A. Br.		X								
rostaffinskii Hansg.										

TABLE 6. Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966 (*continued*)

SPECIES	1	2	*Tabebuia rigida* 6	7	8	3	*Ocotea spathulata* 4	9	*Miconia pachyphylla* 5	*Cyathea pubescens* 10
Nostocales										
Anabaena										
anomala Fritsch										X
laxa (Rabenh.) A. Br.					X					
oscillarioides Bory ex Born. & Flah.										X
oryzae Fritsch						X				
sp.	X	X								
Calothrix										
epiphytica W. & G. West	X									
weberi Schmidle								X		
Coelosphaerium										
dubium Grun.			X							
Gloeotrichia										
echinulata (J. E. Sm.) Richter							X			
longiarticulata G. S. West							X			
Lyngbya										
limnetica Lemm.		X			X					
Microchaete										
uberrima Carter									X	
Oscillatoria										
agardhii Gom.		X								
annae van Goor					X					
limnetica Lemm.				X						
sp.					X		X			
Phormidium									X	
tenue (Menegh.) Gom.				X						
Pseudanabaena					X					
catenata Lauterb.										
constricta (Szafer) Lauterb.		X		X						
Schizothrix										
ericetorum Lemm.		X								
Scytonema										
amplum W. & G. West			X							
burmanicum Skuja						X				
hofmannii C. Ag. ex Born. & Flah.	X									
stuposum (Kütz.) Born. ex Born. & Flah.								X		
tolypothricoides Kütz. ex Born. & Flah.								X		
Scytonematopsis										
kashyapii (Bharadw.) Geitler					X					
Spirulina										
subtilissima Kütz.		X								

TABLE 6. Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966 (*continued*)

SPECIES	1	2	*Tabebuia rigida* 6	7	8	*Ocotea spathulata* 3	4	*Miconia pachyphylla* 9	5	*Cyathea pubescens* 10
Tolypothrix										
distorta Kütz. ex Born. & Flah.							X			
Pleurocapsales										
Xenococcus										
kerneri Hansg.		X								
Stigonematales										
Camptylonema										
indicum Schmidle						X				
Hapalosiphon										
fontinalis (Ag.) Born.		X								
hibernicus W. & G. West	X									X
intricatus W. & G. West	X	X								
luteolus W. & G. West		X	X		X					
stuhlmannii Hieron.					X					
welwitschii W. & G. West					X				X	
Nostochopsis										
lobatus Wood em. Geitler								X		
Plectonema										
indica Dixit					X					
Stigonema										
aerugineum Tilden					X					
hormoides (Kütz.) Born. & Flah.			X	X	X	X		X	X	
informe Kütz.										
mesentericum Geitler	X	X			X			X		
panniforme Harv. ex Born. & Flah.			X	X						
Stigonema										
turfaceum (Berk.) Cooke ex Born. & Flah.	X									
CHLOROPHYTA										
Chaetophorales										
Protococcus										
viridis C. Ag.		X								
Trentepohlia										
aurea (L.) Martius	X							X		
iolithus (L.) Wallroth					X					
umbrina (Kütz.) Born.						X				
Chlorococcales										
Ankistodesmus										
falcatus (Corda) Ralfs		X								
Characium										
stipitatum (Bachm.) Wille							X			

TABLE 6. **Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966** (*continued*)

SPECIES	1	2	*Tabebuia rigida* 6	7	8	*Ocotea spathulata* 3	4	9	*Miconia pachyphylla* 5	*Cyathea pubescens* 10
Chlorella										
vulgaris Beyerinck		X	X				X			
Chlorococcum										
humicola (Näg.) Rabenh.		X		X	X			X		
Oocystis										
borgei Snow				X						X
pyriformis Prescott					X					X
submarina Lagerheim									X	
Pediastrum										
muticum var. *crenulatum* Prescott		X				X				
Quadrigula										
chodatii (Tanner-Füllemann) G. M. Sm.									X	
lacustris (Chod.) G. M. Sm.									X	
Scenedesmus										
arcuatus var. *platydisca* G. M. Sm.							X			
Tetraedron										
tumidulum (Reinsch) Hansg.						X				
Cylindrocapsales										
Cylindrocapsa										
conferta W. West	X						X			
geminella Wolle									X	
Oedogoniales										
Oedogonium sp.		X								
Sphaeropleales										
Sphaeroplea										
annulina (Roth) C. Ag.								X		
Tetrasporales										
Gloeocystis										
major Gerneck										
vesiculosa Näg.								X	X	
Sphaerocystis						X				
schroeteri (?) Chodat			X						X	X
Tribonematales										
Tribonema										
utriculosum (Kütz.) Hazen		X					X			
Ulotrichales										
Stichococcus										
subtilis (Kütz.) Klercker							X			
Ulothrix										
aequalis Kütz.					X					

TABLE 6. **Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966** (*continued*)

SPECIES	1	2	*Tabebuia rigida* 6	7	8	3	*Ocotea spathulata* 4	9	*Miconia pachyphylla* 5	*Cyathea pubescens* 10
Zygnematales										
Cosmarium dentatum Wolle					X					
Cylindrocystis brebissonii var. *minor* W. & G. West			X	X	X				X	
Hyalotheca undulata Nordst.		X		X						
Mougeotia caimani Transeau					X		X			
floridana Transeau			X							
Netrium digitus (Ehrenb.) Itzigos. & Rothe				X			X			
Zygnemopsis desmidioides (W. & G. West) Transeau			X	X	X					
CHRYSOPHYTA										
Heterococcales										
Peroniella planctonica G. M. Sm.				X						
Pleurogaster lunaris Pascher				X						
Tetragoniella gigas Pascher				X						X
Rhyzochrysidales										
Lagynion reductum Prescott		X								
BACILLARIOPHYTA										
Centrales										
Melosira crenulata (Ehrenb.) Kütz.				X						
Triceratium semicirculare Brightw.										X
undulatum Ehrenb.			X	X			X	X		
Pennales										
Anomoeoneis costata (?) (Kütz.) Hust.				X						
Denticula sp.									X	
Diatoma hiemale (Roth) Heib.					X					
Diatomella balfouriana Grev.	X			X						
Diploneis oculata (Breb.) Cl.										X

TABLE 6. Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966 (*continued*)

SPECIES	1	2	*Tabebuia rigida* 6	7	8	3	*Ocotea spathulata* 4	9	*Miconia pachyphylla* 5	*Cyathea pubescens* 10
Eunotia										
tenella (Grun.) Hust.				X						X
Fragilaria										
lapponica Grun.		X								
Frustulia										
rhomboides var. *capitata* (A. Mayer) Patr.		X	X		X				X	
rhomboides var. *viridula* (Bréb.) Cl.					X					
Nitzschia										
dissipata (Kütz.) Grun.										X
ignorata Krasske				X		X				X
Stauroneis										
ignorata (?) Hust.			X	X						
EUGLENOPHYTA										
Euglenales										
Euglena										
elastica (?) Prescott								X		
polymorpha Dangeard					X					
Glenodinium										
kulczynskii (?) (Wolosz.) Schiller										
Trachelomonas										X
charkowiensis (?) Swirenko							X			
TOTAL NUMBER OF SPECIES	13	31	18	35	30	10	19	16	17	14

KEY TO NUMBERS

1 — gelatinous white colony on *Tabebuia rigida*
2 — gelatinous green colony on *T. rigida*
3 — green gelatinous mass on *Ocotea spathulata*
4 — white gelatinous mass on *O. spathulata*
5 — always wet gelatinous mass on *Miconia pachyphylla*
6 — solid mass on *T. rigida*
7 — gelatinous mass on *T. rigida*
8 — another gelatinous mass on *T. rigida*
9 — green material on dead leaves of *O. spathulata* (on ground)
10 — hard mass growing on dead stump of *Cyathea pubescens*

TABLE 7 qualitatively reflects the major synusia as distributed more randomly. It would appear that moisture, light, and seasonal succession during the wetter months combine to reduce the height effect.

During August, 1966, water from a vascular epiphyte and from the bryophytic tree epiphytes was also sampled. The water from the bromeliad *Vriesea sintenisii* and liquid obtained from squeezing the epiphytic bryophyte sheath on tree trunks was analyzed. In TABLE 8 the species

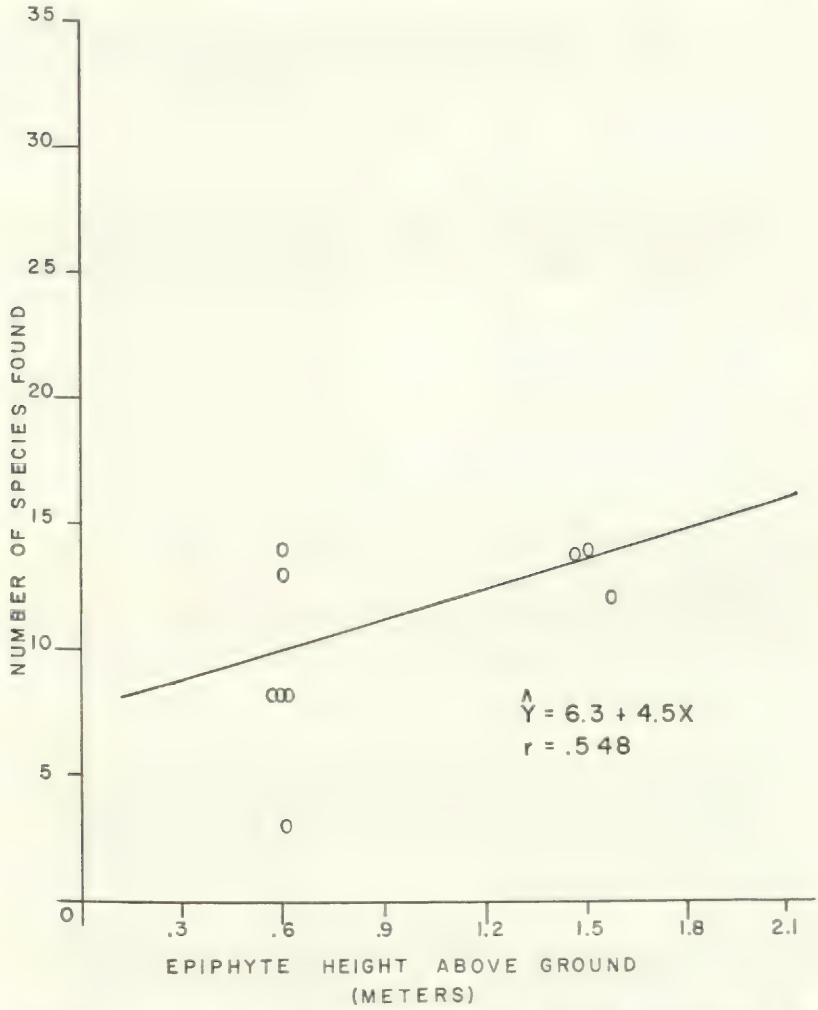

FIGURE 2. Relationship of the height of collection on the vascular host to the number of species from the August, 1966 sampling.

are listed from each sampling. The dominant organisms forming the phyco-synusium in *V. sintenisii* were *Diatoma-Stigeonema-Pithophora*, and the diatom *Diatoma vulgare* was the most prevalent species. The leaves of these epiphytic bromeliads overlap forming a natural catch basin for moisture. The species found in this basin are more predominantly aquatic in nature than species previously reported.

The bryophytic squeezings revealed a synusium dominated by *Diatoma-Eunotia-Chroococcus*. *Diatoma vulgare* was again the dominant species; diatoms were generally more prevalent. The dominance of the

TABLE 7. **Species found on Endemic Vascular Species during August, 1966**

SPECIES	VASCULAR HOST * †
CYANOPHYTA	
Chroococcales	
Aphanocapsa biformis A. Br.	(1) (2)
Aphanothece clathrata W. & G. West	(3)
Chroococcus dispersus (Keissler) Lemm.	(1) (8)
C. minor (Kütz.) Näg.	(5)
C. minutus (Kütz.) Näg.	(1) (3) (5)
C. pallidus Näg.	(3)
C. turgidis (Kütz.) Näg.	(1) (3) (5) (8) (9)
Gloeothece palea (Kütz.) Näg.	(5)
Microcystis aeruginosa Kütz.	(1) (3) (5) (8)
Synecococcus aeruginosus Näg.	(1) (3) (5) (8)
Nostocales	
Anabaena circinalis Rabenh.	(1) (8)
Aulosira prolifica (?) Bharadw.	(1) (2) (5) (9)
Cylindrospermum catenatum (?) Ralfs	(8)
Phormidium tenue (Menegh.) Gom.	(3) (5) (7) (8)
Scytonema javanicum (?) (Kütz.) Born.	(2) (5)
S. schmidtii (?) Gom.	(5)
Stigonematales	
Hapalosiphon luteolus W. & G. West	(3) (possible growth form of *Stigonema hormoides*)
Stigonema dendroideum Frémy	(8)
S. hormoides (Kütz.) Born. & Flah.	(1) (2) (3) (4)
S. panniforme (C. Ag.) Harv.	(5)
CHLOROPHYTA	
Zygnematales	
Zygnemopsis desmidioides (W. & G. West) Transeau	(2)
BACILLARIOPHYTA	
Centrales	
Biddulphia alternans (Bail.) Van Huerck	(2) (4)
Campylodiscus echeneis (?) Ehrenb.	(3) (5)
Cyclotella glomerata Bachn.	(7) (9)
Melosira crenulata (Ehrenb.) Kütz.	(1)
M. granulata (Ehrenb.) Ralfs	(6) (9)
M. varians C. Ag.	(3) (possible auxospore noted)
Pennales	
Cymbella ventricosa Kütz.	(7) (9)
Eunotia exigua (?) (Bréb) Rabenh.	(3) (4) (8)
E. naegelii Mig.	(7) (9)
E. perpusilla (?) Grun.	(4)
E. praerupta Ehrenb.	(3) (9)
E. tenella (Grun.) Hust.	(7) (9)
Frustulia rhomboides var. *capitata* (Mayer) Patr.	(1) (2) (4) (5) (6) (7) (8) (9)
F. rhomboides var. *saxonica* (Rabenh.) DeToni	(2) (4) (9)
F. rhomboides var. *viridula* (Bréb.) Cl.	(8)
Isthmia enervis Ehrenb.	(9)

TABLE 7. Species found on Endemic Vascular Species during August, 1966 (*continued*)

SPECIES	VASCULAR HOST * †
Navicula carniolensis (?) Hust.	(7)
N. crucicula (?) (W. Smith) Donk	(9)
N. cryptocephala (?) Kütz.	(8)
N. tenelloides Hust.	(4) (6)
Navicula sp. (radiate, capitate form)	(8)
N. sp. (different from above)	(9)
Nitzschia dissipata (Kütz.) Grun.	(4)
N. hantzschiana Rabenh.	(8)
N. sp.	(1) (5)
Pinnularia sudetica Hilse	(7)
Rhopalodia gibberula Mueller	(1) (8) (9)
Surirella ovata Kütz.	(1)

* The numbers identify the vascular host species as follows: (1), (2), (7), (8), *Tabebuia rigida*; (3), (4), (9), *Ocotea spathulata*; (5), *Miconia pachyphylla*; (6), *Cyathea pubescens*.

† For relative position of sample on vascular host see Table 5.

TABLE 8. Algal Species Components of Non-algal Epiphytes Collected in August, 1966

SPECIES	BROMELIAD	BRYOPHYTE SQUEEZINGS
CYANOPHYTA		
Chroococcales		
Aphanocapsa grevillei (Hass.) Rabenh.	X	
Chroococcus dispersus var. *minor* G. M. Sm.	X	
C. minor (Kütz.) Näg.	X	X
C. minutus (Kütz.) Näg.	X	X
C. turgidus (Kütz.) Näg.	X	X
C. varius A. Br.	X	
Dactylococcopsis fascicularis Lemm.	X	
Gloeocapsa aeruginosa (Carm.) Kütz.		X
Gloeothece palea (Kütz.) Rabenh.		X
Merismopedia elegans A. Br.	X	
Microcystis orissica (?) W. West		X
Synechococcus aeruginosus Näg.	X	X
Nostocales		
Aulosira prolifica Bharadw.		X
Nostoc muscorum C. Ag.	X	
Oscillatoria geitleriana Elenkin		X
O. subbrevis Schmidle		X
Pleurocapsales		
Myxosarcina spectabilis Geitler	X	
Stigonematales		
Hapalosiphon delicatulus W. & G. West	X	
H. welwitschia W. & G. West		X
Stigonema aerugineum Tilden	X	
S. hormoides (Kütz.) Born. & Flah.	X	X
S. minutum (C. Ag.) Hass.		X

TABLE 8. Algal Species Components of Non-algal Epiphytes Collected in August, 1966 (*continued*)

SPECIES	BROMELIAD	BRYOPHYTE SQUEEZINGS
CHLOROPHYTA		
Chaetophorales		
Cephaleuros virescens Kunze		X
Protococcus viridis C. Ag.	X	X
Stigeoclonium polymorphum (?) (Franke) Heering	X	
Trentepohlia aurea var. *tenuior* Brühl & Biswas	X	
T. aurea (L.) Martius	X	
T. torulosa De Wildeman	X	
Chlorococcales		
Characium obtusum (?) Braun	X	
Chlorella ellipsoidea Gern.	X	
Crucigenia quadrata Morren	X	
Pediastrum muticum Kütz.	X	
Trochiscia granulata (Reinsch) Hansg.	X	
Cylindrocapsales		
Cylindrocapsa conferta W. West	X	
Oedogoniales		
Pithophora oedogonia (Mont.) Wittr.	X	
Tribonematales		
Tribonema utriculosum (Kütz.) Hazen	X	
Ulotrichales		
Geminella interrupta Turpin	X	
Zygnematales		
Micrasterias denticulata (?) Bréb.	X	
Mougeotia globulispora Jao		X
Temnogametum transeaui Prescott	X	
Zygogonium ericetorum Kütz.		X
BACILLARIOPHYTA		
Centrales		
Coccinodiscus lacustris (?) Grun.		X
Cyclotella bodanica (?) Eulenst.	X	
Melosira crenulata (Ehrenb.) Kütz.	X	
M. granulata (Ehrenb.) Ralfs	X	
Triceratium semicirculare Brightw.	X	X
Pennales		
Amphora ovalis Kütz.		X
Diatoma hiemale (Roth) Heib.	X	X
D. hiemale var. *mesodon* (Ehrenb.) Grun.	X	
Diatoma tenue var. *elongatum* Lyngb.	X	
D. vulgare Bory	X	X
Eunotia pectinalis f. *elongata* Van Huerck	X	
E. pectinalis var. *minor* (Kütz.) Rabenh.		X
E. soleirolii (Kütz.) Rabenh.		X
E. tenella (?) (Grun.) Hust.		X
Fragilaria brevistriata Grun.		X

TABLE 8. **Algal Species Components of Non-algal Epiphytes Collected in August, 1966** (*continued*)

SPECIES	BROMELIAD	BRYOPHYTE SQUEEZINGS
Frustulia rhomboides var. *capitata* (Mayer) Patr.		X
Hantzschia amphioxys (Ehrenb.) Grun.	X	X
Navicula sp.	X	X
Nitzschia tryblionella Hantzsch.		X
Surirella ovata Kütz.		X
Tropidoneis sp.		X
PYRROPHYTA		
Dinococcales		
Cystodinum cornifax (Schilling) Klebs	X	
TOTAL NUMBER OF SPECIES	42	32

diatoms plus the fact that the trunks of the vascular hosts transmit to the ground 21.4 per cent of the rainfall reaching the forest canopy may be one of the principal factors in determining the presence of this diatom-dominant association.

During February of 1968, mucilaginous material from around aërial roots of *Hedyosmum arborescens* was analyzed for algal components. One sample was fluid, containing a large amount of water, while the second sample was highly consolidated and, in comparison to the other sample, low in water. TABLE 9 compares the algal species found in the two samples differing in moisture content. The sample containing the most moisture (1) has the highest number of species. Species such as *Trentepohlia aurea*, *Melosira varians*, and *Frustulia rhomboides* var. *capitata* are represented in both samples. Throughout the entire study these species have exhibited eurybiont characteristics. The green alga *T. aurea* was the major component in both samples, while none of the other species appeared more than occasionally.

As a gross ecological parameter the height above the ground seems to become a limiting factor to many diatoms and blue-green algae. Height would include the above mentioned factors of light, moisture, and temperature as well as many others. A general shift from a Bacillariophyta-dominated to a Cyanophyta-dominated to a Chlorophyta-dominated algal synusium is noted as samples are taken from points higher above the ground.

In concluding, it is important to compare the regression and correlation analyses of the February-March, 1966, to August, 1966, samples. A shift in environmental utilization is evident. This could be called a seasonal response and it may be a reaction to light attenuation caused by increased cloudiness during August. It is possible that the algal species are re-distributing to a higher portion of the vascular stem in response to a more favorable light condition. Only samples taken at higher levels

TABLE 9. **Algal Species Found among Mucilaginous aërial root secretions of Hedyosmum arborescens**

SPECIES	SAMPLE NUMBER *	
CYANOPHYTA		
Chroococcales		
Chroococcus dispersus (Keissler) Lemm.	1	
C. turgidis (Kütz.) Näg.		2
Microcystis ramosa Bharadw.	1	
Nostocales		
Anabaena circinalis (?) Rabenh.	1	
Aulosira prolifica (?) Bharadw.	1	
Oscillatoria foreaui (?) Frémy		2
Stigonematales		
Stigonema hormoides (Kütz.) Born. & Flah.	1	
CHLOROPHYTA		
Chaetophorales		
Protococcus viridis C. Ag.	1	
Trentepohlia aurea var. *tenuior* Brühl & Biswas	1	2
Chlorococcales		
Chlorella-like	1	
BACILLARIOPHYTA		
Centrales		
Biddulphia alternans (J. W. Bailey) Van Heurck	1	
Melosira varians C. Ag.	1	2
Pennales		
Eunotia fallax Cleve-Euler	1	
Frustulia rhomboides var. *capitata* (Mayer) Patr.	1	2
Navicula cincta (Grun.) Cl.	1	
N. contenta Grun.	1	
Nitzschia parvula Lewis		2
TOTAL NUMBER OF SPECIES	14	6

* Sample (1) refers to a very watery mucoid material, and Sample (2) refers to a very thick and highly viscous mucoid material.

on these stems would help resolve this apparent successional shift. What is important to note is that a shift occurs and that it appears to be related more to light attenuation than to other factors.

In further comparison of FIGURES 1 and 2 it is evident that the number of species has declined. This is reinforced by the number of species reported in TABLES 6 and 7. It would appear that during February-March 1966, a more favorable set of environmental conditions existed than in August when reduction in numbers of species was evident.

Finally, it is important to report other observations concerning distribution of diatoms and green algae. Diatoms have certain water requirements (Lund, 1945). Their distribution on the vascular hosts when samples from February-March, 1966, are compared to August, 1966, may not directly reflect a "wetness" requirement but may be re-

lated to the amount and duration of light, which is affected by moisture in the form of clouds and fog. Further, Fritsch (1922) reported *Trentepohlia* to be very resistant to fluctuating moisture. Therefore, *Trentepohlia* dominance higher on the vascular trunk may be related not only to a tolerance for changing moisture but also to a higher light tolerance (or requirement).

In all the investigations of nearly aquatic ground samples and highly moist aërial roots there is a high incidence of diatoms, while samples from drier habitats shift to non-diatom dominant forms. It is reasonable to conclude on the basis of the samples investigated that the large number of algal epiphyte species studied have become successfully established and exist in distinct microhabitats. The algae exhibit seasonal variation in possible response to meteorological conditions. The gross ecological parameter of height above the ground appears to be a proper method of assessing environmental influences in a vertical direction.

SUMMARY

The cloud forest can be likened to a large natural culture unit having uniformly constant meteorological conditions, and, judging from the relatively large number of species found, adequate nutrients. Though all would appear uniform at the first casual investigation, careful analysis indicates that the subaërial algal epiphytes are not uniformly distributed, but are segregated into phyco-synusia. These seem to be microhabitats related to height above the ground and type of host material. The data depict an apparent random horizontal distribution but a less random vertical pattern of distribution. This vertical distribution and apparent seasonal succession pattern appears related to slight changes in meteorological conditions. Samples taken higher on a tree trunk during drier months contain fewer species than those collected closer to the ground. The probability exists that epiphytes located higher above the ground are subjected to greater fluctuations in temperature, moisture, and light. However, the lower parts of a tree trunk are older and perhaps more stable chemically. Further, during wetter months the species-count on the host appears to be rearranged and seasonal species variation appears. During this period increased cloud cover and fog reduce light penetration which may be instrumental in this change.

Subaërial epiphytic algal growth in all samples studied, and especially on the four principle vascular host species in the Luquillo elfin forest on Pico del Oeste, appears not as a uniformly distributed algal veneer, but rather as associations of species representing various intergrading microhabitats.

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A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR *

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18. **Rochelia** Reichenb. Flora 7: 243. 1824; Icon. Crit. 2: 13. *t. 123.* 1824.

Raclathris Raf. Sylva Tellur. 167. 1838.

TYPE SPECIES: *R. saccharata* Reichenb.

Usually annual, rarely biennial, villous or hispid herbs. Leaves alternate. Inflorescence terminal, simple or branched, bracteate. Flowers small, blue or white. Calyx usually 5-fid or rarely 9–10-fid (not in the West Pakistan or Kashmir species), usually enlarged in fruit, lobes linear, oblong or lanceolate, rounded auricled or sagittate at the base. Corolla small, campanulate, infundibuliform or tubular, tube usually cylindric, throat with or without appendages, lobes small, spreading. Stamens 5, included; anthers ovate, usually obtuse. Gynobase columnar, slightly developed; style filiform, stigma indistinctly capitate. Nutlets 2, 1-seeded, oblong to oblong-ovate, glabrous, smooth to tuberculate, affixed along the whole length of the gynobase.

A genus of about 15 species, centering in southwestern Asia and ranging from central Asia to the Mediterranean basin. One species occurs in Australia.

KEY TO THE SPECIES

a. Nutlets glabrous, smooth, shining. ..... 1. *R. leiocarpa.*
a. Nutlets minutely tuberculate to stellate-papillose.
  b. Calyx lobes ovate-lanceolate in fruit, auriculate-cordate at base. ..... 2. *R. cardiosepala.*
  b. Calyx lobes oblong to linear-lanceolate or linear in fruit, never auriculate-cordate at base.
    c. Calyx lobes 6–7 mm. long in fruit, erect or slightly recurved at apex, strongly narrowed towards the base, subunguiculate, midrib well developed and covered with stiff erect trichomes. ... 3. *R. macrocalyx.*
    c. Calyx lobes 2–5(–6) mm. long in fruit, recurved at apex or throughout their length, not narrowed towards the base, roundish, not unguiculate, midrib poorly developed, trichomes various.
      d. Pedicel 10–15 mm. long in fruit, at minimum twice the length of calyx. ..... 4. *R. peduncularis.*
      d. Pedicel 3–8 mm. long in fruit, at maximum not twice the length of calyx.
        e. Pedicel in fruit shorter or subequalling the calyx. ..... 5. *R. disperma.*

* Continued from volume 51, p. 520.

e. Pedicel in fruit always longer than the calyx.
f. Calyx lobes, in fruit, longer to much longer than the nutlets; style exceeding the nutlets by 0.5–1 mm. ..... 6. *R. stylaris.*
f. Calyx lobes in fruit usually shorter than or equal to, rarely longer than the nutlets; style exceeding the nutlets by 0.5 mm.
g. Calyx lobes linear in fruit, to 0.3 mm. broad, curved, bearing usually straight, sometimes slightly curved, trichomes; nutlets 2–2.5 mm. long, attached subhorizontally. ..... 7. *R. bungei.*
g. Calyx lobes oblong-lanceolate in fruit, 0.5–0.8 mm. broad, usually erect, sometimes curved, bearing usually uncinate, sometimes curved, trichomes; nutlets 3–3.5 mm. long, attached vertically or slightly tilted. ..... 8. *R. laxa.*

1. **R. leiocarpa** Ledeb. Fl. Alt. 1: 172. 1829; DC. Prodr. 10: 176. 1846; Boiss. Fl. Orient. 4: 245. 1875; M. Pop. Fl. URSS 19: 557. 1953.

R. incana Kar. & Kir. Bull. Soc. Nat. Moscou 15: 710. 1841.
R. stellulata var. Kar. & Kir. *loc. cit.*
R. lissocarpa Dunn, Kew Bull. 1924: 386. 1924, *syn. nov.*

TYPE: Hab. in sterilibus ad fl. Kurtschum deserti Soongaro-Kirghisici orientalis, without citation of collector's name (B).

ICON.: Ledeb. Icon. Pl. Fl. Rossica 3: *t. 244.* 1847; M. Pop. l. c. 19: *t. 27. fig. 4.* 1953.

Annual, erect herb, branched near the base, 5–25 cm. tall. Stem and branches slender, brownish, covered loosely with short, appressed, antrorse, white trichomes. Basal leaves sessile, linear, oblong-ovate or oblong–spathulate, entire, obtuse, 10–25 mm. long, 1–2 mm. broad, covered on both surfaces with thin, spreading white trichomes 0.2–0.7 mm. long, arising from large tuberculate bases, lower surfaces sometimes less hairy or rarely subglabrous; cauline leaves gradually decreasing in size upwards. Inflorescence lax, unilateral, short in flower, elongated in fruit, bracteate, bracts lanceolate, acutish. Flowers subsessile, fruits pedicellate, pedicels up to 2.5 mm. long, deflexed. Calyx divided nearly to the base, lobes lanceolate, erect, 1–1.5 mm. long in flower, linear, elongated to 4 mm., curved their whole length, pubescent in fruit, trichomes straight to slightly curved or sometimes uncinate. Corolla blue, campanulate, slightly narrowed at the throat, tube nearly equal to the calyx, lobes ovate to rotundate, erect or patent, 0.5 mm. long. Nutlets 2, yellowish- to pinkish-white, glabrous, smooth, shining, 2 mm. long. Style exceeding the nutlets by 0.5 mm.

DISTRIBUTION: Soongaria, Turkestan, West Pakistan, Kashmir.

West Pakistan: GILGIT AGENCY: Gurais valley, Minimorg, 3000 m., *Inayat 25716* (K); Baltistan, upper end of Hushe valley, Chondakoro glacier basin, at

the foot of the Masherbrum, hillside near base camp Shahircho, 3650 m., *Webster & Nasir 5974* (GH, RAW).

Kashmir: UPPER KISHENGANGA VALLEY: Purane Tilal, *R. R. Stewart 4398* (RAW, K-type of *R. lissocarpa* Dunn).

The specimens of *Rochelia leiocarpa* are usually mixed with those of *R. bungei* in the collections cited above. *Rochelia leiocarpa* is very closely related to *R. bungei* from which it can easily be distinguished by its smooth, glabrous, shining nutlets.

2. **R. cardiosepala** Bunge, Mém. Acad. Sci. St. Pétersb. Savants Étr. 7: 420. 1851; Boiss. Fl. Orient. 4: 246. 1875; C. B. Clarke in Hook. f. Fl. Brit. India 4: 166. 1883; M. Pop. Fl. URSS. 19: 563. 1953; Riedl in Rechinger, Fl. Iranica 48: 90. 1967.

TYPE: In rupibus graniticis ad Bakali Turkestaniae, *Lehmann s.n.* (LE).

ICON.: M. Pop. l. c. 19: *t. 27. fig. 1.* 1953.

Annual, up to 35 cm. tall. Stem and branches covered loosely or densely with antrorsely appressed, short, white trichomes. Basal and lower cauline leaves to 80 mm. long and 7 mm. broad, oblong-ovate to spathulate, entire, sometimes slightly revolute at the margins, obtuse to roundish at apex, gradually attenuated at base into a broad petiole to 50 mm. long; both surfaces covered with spreading, thin, white trichomes, to 1 mm. long, arising from tuberculate bases; upper cauline leaves sessile, obtuse to sometimes acute, gradually decreasing in size upwards. Inflorescence lax, simple or branched, bracteate, bracts leaflike. Pedicels erect, densely hairy, to 2 mm. long in flower, elongated to 4 mm. in fruit, curved, densely pubescent, trichomes usually uncinate. Calyx divided nearly to the base, lobes in flower ca. 2 mm. long and 0.7 mm. broad, lanceolate, much enlarged in fruit, to 6 mm. long and 4.5 mm. broad, acute, erect, auriculate-cordate at base. Corolla pale blue to purple-blue, ca. 3 mm. long, subcylindric, narrowed at the throat, tube usually equalling the calyx, lobes ovate to roundish, suberect to patent. Nutlets 2, grayish-green, to 4 mm. long, stellate-papillose.

DISTRIBUTION: Iraq, Iran, Afghanistan, West Pakistan, Kashmir, northwest India; Caucasus, Turkestan, Pamir Alaj, Kizil Kum, Syr Darya, Amu Darya, Dsungaro-Tarbagatai, Tien Shan.

West Pakistan: CHITRAL STATE: Drosh, 1500 m., *Stainton 2277* (BM). SWAT STATE: Jabba Valley, *Rechinger 30733a, 30761* (W); between Saidu Sharif and Baherain, about 5 miles from Baherain, *Kazmi s.n.* (PES). Reported from: GILGIT AGENCY: Astor district, Gudai, *R. R. Stewart*; Baltistan, Marpu Nullah, *Duthie 11839*.

Kashmir: Purane Tilal, 2600 m., *R. R. & I. D. Stewart 4448* (K, MICH); Srinagar, 1700 m., *R. R. Stewart 12546* (GH).

3. **R. macrocalyx** Bunge, Mém. Acad. Sci. St. Pétersb. Savants Étr. 7: 419. 1851; Boiss. Fl. Orient. 4: 246. 1875; M. Pop. Fl. URSS 19: 562. 1953; Riedl in Rechinger, Fl. Iranica 48: 92. 1967.

R. rectipes Stocks in Jour. Bot. Hook. **4**: 176. 1852; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 166. 1883.

TYPE: In rupestribus granites Turkestaniae ad Balsali, *Lehmann s.n.* (LE).

ICON.: M. Pop. Fl. URSS **19**: *t. 27. fig. 3.* 1953.

Annual, erect or decumbent herb, up to 15 cm. tall. Stems many, much branched, branches short, both stem and branches usually covered with straight, sometimes curved, thin, spreading trichomes to 1 mm. long, which may arise from conspicuous tuberculate bases on the lower part of the stem. Basal leaves obtuse or roundish, slightly attenuated at base, to 1 cm. long and 1.5–2.5 mm. broad, covered on both sides with trichomes like those of the stems, arising from tuberculate bases; cauline leaves narrower, usually longer than the basal leaves. Inflorescence, lax, few-flowered, bracteate. Pedicels in flower short, in fruit elongated to 7–12 mm., narrowed towards the base, hairy, trichomes spreading. Calyx divided to the base, lobes lanceolate, acute, 6–7 mm. long, 1.5–2 mm. broad in fruit, narrowed towards the base into a short claw, usually 0.5–1 mm. long, stout, midrib prominent below, covered on both sides with short, erect trichomes (sometimes arising from tuberculate bases). Corolla blue, cylindrical, narrowed at the throat, ca. 1.5 mm. long, lobes short, suberect. Nutlets bluish-white to light brown, ca. 3.5 mm. long, 1.5–2 mm. broad at base, densely stellate-papillose. Style exceeding the nutlets by ca. 1 mm.

DISTRIBUTION: Iran, Afghanistan, West Pakistan, Kashmir, northwest India, Pamir Alaj, Kizil Kum.

West Pakistan: KALAT STATE: near Surab, *Kazmi 1303b* (PES); *Rechinger 28329* (W). QUETTA DIST.: 5 miles west of Ziarat, *Kazmi s.n.* (PES); Ziarat proper, 2600 m., *Jafri & Akbar 2124* (E); Spin Karez, *Kazmi 1618b* (PES); *Rechinger 29213* (W). Reported from: QUETTA: Inter Bostan et Saran Tangai, 1800 m., *Rechinger 29174* (W); in jugo W. Ziarat in junipereis, 2200 m., *Rechinger 29335* (W); Baluchistan, Gurghina, *Stocks s.n.*

Kashmir: Zaskar, Char, Ichor, 4300 m., *Koelz 5663* (GH, MICH, US); Kargia, Kargah, 4500 m., *Koelz 5581* (GH, MICH, US).

4. **R. peduncularis** Boiss. Diagn. Pl. Orient. **7**: 35. 1846; Fl. Orient. **4**: 246. 1875; M. Pop. Fl. URSS **19**: 561. 1953; Riedl in Rechinger, Fl. Iranica **48**: 91. 1967.

TYPE: In humidis alpis Kuh Delu, Persiae australis *Kotschy 531a* (W).

ICON.: M. Pop. Fl. URSS **19**: *t. 27. fig. 2.* 1953.

Annual, erect herb, to 20 cm. tall. Stems simple or branched above, covered with short, white, subpatent trichomes. Basal leaves few, sessile, oblong, obtuse or roundish, entire, sometimes slightly revolute at margins, to 2 cm. long and 2–3 mm. broad, both sides covered with, thin, short, spreading white trichomes, usually arising from tuberculate bases; cauline leaves narrower and longer, upper cauline leaves shorter and broader, usually acute. Inflorescence lax, few flowered, bracts minute. Pedicels

1–3.5 mm. long in flower, patent, gradually narrowed towards the base, elongated to 8–15 mm. in fruit, hairy, trichomes short, erect. Calyx divided nearly to the base, lobes broad, lanceolate, erect, hairy, ca. 2 mm. long, 0.5 mm. in flower, broad, subpatent, the upper half curved, with stout and prominent midrib and patent trichomes 4–6 mm. long, to 1.5 mm. in fruit. Corolla blue, subcylindrical, narrowed at the throat, ca. 2.5 mm. long, tube equalling the calyx, lobes small, ovate to orbicular, suberect. Nutlets 2, white to grayish, ovate, 2–2.5 mm. long, stellate-papillose. Style exceeding the nutlets by about 0.7 mm.

DISTRIBUTION: Iran, Afghanistan, West Pakistan, Kashmir ?, Pamir Alaj, Tien Shan.

West Pakistan: CHITRAL STATE: Lutko, 2550 m., *Bowes Lyon 879* (BM). QUETTA DIST.: Quetta to Ziarat, at the top of Pass, 2200 m., *Kazmi 1660a* (PES); *Lamond 1170* (E); *Rechinger 29317* (W); Spin Karez, 1900 m., *Kazmi 1632b* (PES); *Rechinger 29210* (W).

5. **R. disperma** (L. f.) C. Koch, Linnaea 22: 649. 1849, emend. Karyagin, Isv. Akad. Nauk Azerb. USSR 12: 13, 14. 1945; M. Pop. Fl. URSS 19: 551. 1953; Riedl in Rechinger, Fl. Iranica 48: 94. 1967.

Lithospermum dispermum L. f. Descr. Pl. Rar. 13. 1762.
Rochelia stellulata Boiss. Fl. Orient. 4: 244. 1875, *pro parte* non Reichenb. 1824.

TYPE: "Habitat in Hispania inter Gaditanum et Madritium," without citation of collector's name, Herb. No. 181.11, 181.12 (LINN).
ICON.: L. f. l. c. *t.* 7. 1762.

Annual, erect or decumbent, to 20 cm. tall. Stem usually branched at the base or sometimes above, branches long, slender; stem and branches covered with short, appressed to subappressed, white trichomes, only those near the base arising from tuberculate bases. Basal leaves ovate to oblong-ovate, entire, roundish, attenuated towards the base, 5–7 mm. long, 2–3 mm. broad, both sides covered with scattered short, thin, erect, white trichomes; lower cauline leaves linear-lanceolate, obtuse, 12–30 mm. long, 1–3.5 mm. broad; upper cauline leaves gradually decreasing in size, more pubescent. Inflorescence short in flower, later elongated to 15 cm., bearing distant unilateral fruits; bracteate, bracts small. Pedicels in flower lacking to very short, to 0.5 mm. long, much elongated in fruit, 1.5–2.5 mm. long, always shorter than the calyx, horizontal or recurved, pubescent, trichomes sometimes uncinate. Calyx divided to the base, lobes linear, ca. 1.5 mm. long and 0.2 mm. broad in flower, densely pubescent, erect, to 5 mm. long, curved their whole length or at least the upper half, equalling or longer than the pedicels, densely pubescent with spreading, sometimes uncinate, trichomes in fruit. Corolla blue, subtubular, usually exceeding the calyx, 1.5–1.7 mm. long, lobes small, ovate to rounded, suberect. Nutlets 2, subhorizontal, white, stellate-papillose. Style exceeding the nutlets by 0.5–1 mm.

DISTRIBUTION: Turkish Armenia, Caucasus, Iraq, Iran, Afghanistan, West Pakistan, Kashmir, Turkestan.

West Pakistan: KURRAM AGENCY: Kurram Valley, Parachinar, *Kazmi s.n.* (PES); *R. R. Stewart 28942, 28955* (RAW); without locality, *Harsukh 14747* (K). QUETTA DIST.: Spin Karez, 1900 m., *Kazmi 1632* (GH, PES); Quetta to Ziarat, at the top of Pass, 2200 m., *Lamond 1172* (E); Ziarat, *Jafri & Akber 2115* (E); Tatli, near Loralai, *Nath 6028, 6034* (RAW). SHAHPUR DIST.: Manza Pahl, 16. 4. 1904, *Drummond* Herb. Kew no. *20432* (E). WAZIRISTAN AGENCY: Wana, *Kazmi s.n.* (PES); Miram Shah, *Kazmi 190b* (PES); near Datta Khel, *Kazmi 185b* (PES). Reported from: South Waziristan: Kaniguram, *J. L. Stewart s.n.*; Baluchistan, *Stocks s.n.*; GILGIT AGENCY: Naltar Valley, *R. R. Stewart 26339*; Baltistan, *Ludlow s.n.*

Kashmir: Reported from: Nubra, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.*

Closely related to *Rochelia disperma* is *R. bungei* from which the former is differentiated by its pedicels always shorter or sometimes subequal to the calyx in fruit, its much longer fruiting calyx lobes (up to 5 mm.) and its subhorizontally attached nutlets. In *R. bungei* the fruiting pedicels are always longer than the calyx, the calyx lobes in fruit do not exceed 2 mm. in length, and the nutlets are attached horizontally.

Rochelia stellulata Reichenb. in Hook. f. Fl. Brit. India **4**: 166. 1883, is a misidentification.

6. **R. stylaris** Boiss. Fl. Orient. **4**: 245. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 166. 1883; Riedl in Rechinger, Fl. Iranica **48**: 93. 1967.

TYPE: Afghanistan: circa Pusht, *Griffith s.n.* (K-holotype, W-isotype).

ICON.: Riedl in Køie & Rechinger, Biol. Skr. 13(4): *fig. 196, 197*. 1963.

Annual, usually erect, sometimes decumbent herb, to 15 cm. tall. Stems many, branched, branches long, spreading, stem and branches covered with short, thin, subappressed trichomes. Basal leaves many, petiolate, oblong-spathulate, obtuse to rotundate, entire, gradually narrowed toward the petioles, petiole longer, equal to, or shorter than the lamina, (including petioles) to 35 mm. long and 5(–6) mm. broad, both surfaces covered with thin, short, patent, white trichomes arising from prominent tuberculate bases; middle cauline leaves sessile, linear to linear-oblong; upper cauline leaves much shorter and narrower. Inflorescence lax, bearing many unilateral flowers, much elongated in fruit. Pedicels in flower 1–1.5 mm. long, hairy, erect, to 6 mm. long, slender, pubescent, usually recurved in fruit. Calyx divided nearly to the base, lobes lanceolate, 1–1.5 mm. long in flower, nearly equalling the corolla, pubescent, erect, linear, curved inside, especially at the tips, spreading, to 4 mm. long in fruit. Corolla bluish-white to blue, equal or slightly exceeding the calyx lobes, ca. 2 mm. long, cylindrical, lobes short, suberect. Nutlets 2, grayish, 2–2.5 mm. long, recurved, attached subhorizontally, much shorter than the enlarged calyx, stellate-papillose. Style exceeding the nutlets by 0.5–0.8 mm.

DISTRIBUTION: Afghanistan, West Pakistan, Kashmir, northwestern India.

West Pakistan: ATTOCK DIST.: Hasan Abdal, *R. R. Stewart 6970* (K, MICH); *Kazmi s.n.* (PES); *Dickason 69* (MICH); *Aitchison 475* (K). CHITRAL STATE: Mastuj track, Barenis, 2000 m., *Stainton 2420* (BM); Drosh, *Stainton 2277* (BM). JHELUM DIST.: Salt Range, Sone Sihian Valley? (Sayedan Valley), *Fleming 29* (E). KHYBER AGENCY: Ali Masjid, *Kazmi s.n.* (PES); near Landi Kotal, *Kazmi 2500* (PES); Khyber Pass, Torsapper, 1760 m., *H. H. Johnston 60* (E); Khyber Pass, *H. H. Johnston 13, 44, 45* (E). Dry rocky area near Afghan border, *R. J. Rodin 2563* (US). KURRAM AGENCY: south of Parachinar, *Kazmi 2506* (PES). PESHAWAR DIST.: near Palosi village, *Kazmi 2489* (PES); between Peshawar and Pabbi, *Kazmi 2525* (PES); Peshawar, *J. L. Stewart 137* (GH); *Vicary s.n.* (with a note) (K); QUETTA DIST.: between Yaro and Saranan, on Quetta-Chaman Rd., *Kazmi 1490b* (PES). RAWALPINDI DIST.: Rawalpindi, *R. R. Stewart s.n.* (K); Rawalpindi, Topi Park, *Kazmi 2517* (PES); *R. R. Stewart 14587* (GH, US); Margalla, north of Rawalpindi, *Pinfold 19* (BM); *Dickason 68* (MICH); Harroo, *Aitchison 1080* (K); Fattehjung (13–3–1872), *Aitchison s.n.* (K); Islamabad, rocks at the foot of Paracharian, *Kazmi 2537* (PES). SWAT STATE: near Mingora, *Kazmi 2478* (PES). Swat Border Post, *R. R. Stewart 27420* (RAW); Manglaur, 1000 m., *R. R. Stewart 27420a* (BM). WAZIRISTAN AGENCY: Miran Shah, *Kazmi s.n.* (PES). Reported from: Quetta, *Suzuka s.n.*; Bolan Pass, *Rechinger 28425*; Kurram Valley, Shalizan, *Aitchison 140*; GILGIT AGENCY: Bagrot Valley, *Conway s.n.*; *Nakao s.n.*; Hunza State, *Russell s.n.*

Kashmir: PURIG: Parkochin, *Koelz 5993B* (MICH); Srinagar, *R. R. Stewart 11088* (GH); between Kohala and Muzzaffarabad, *Kazmi 2518* (PES); Muzzaffarabad, *Kazmi 2535* (PES). Miscellaneous: Kashmir, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH); Kashmir (22. 4. 1848), *Thomson s.n.* (K). Reported from: Gulmarg, *R. R. Stewart s.n.*; Ladak, Lamayurun, *Osmaston 139*.

7. **R. bungei** Trautv. Acta Horti Petrop. 9(2): 462. 1886; M. Pop. Fl. URSS 19: 554. 1953; Riedl in Rechinger, Fl. Iranica 48: 93. 1967.

TYPE: Turcomania: Kisil-Arwat, *Becker s.n.* (LE).

Annual, usually simple, erect, but sometimes sparsely branched and decumbent herbs, 8–20(–30) cm. tall. Stem and branches slender, covered on the lower part with patent, on the upper part with subappressed to appressed, thin, white trichomes to 0.7 mm. long. Basal leaves obovate, roundish at apices, entire, attenuated towards the bases, 3–5 mm. long and 1–2 mm. broad, covered on both surfaces with thin, white spreading trichomes, arising from tuberculate bases; middle cauline leaves oblong to linear-lanceolate, acutish, 7–20 mm. long, 1–2 mm. broad; upper cauline leaves shorter and broader. Inflorescence lax, bracteate. Pedicels in flower to 0.7 mm. long, in fruit elongated to 4 mm., slender, recurved, narrowed and usually twisted at the base, sometimes falling with old fruits. Calyx divided to the base, lobes linear, 1.5–2 mm. long in flower, not much elongated in fruit, linear, shorter than the pedicel, curved inside throughout its length, holding the nutlets, pubescent with short, usually straight, rarely curved, never uncinate trichomes. Corolla blue, tubular, 1.5–2 mm.

long, lobes short, suberect. Nutlets 2, yellowish-white, 2–2.5 mm. long, nearly horizontal, stellate-papillose. Stigma exceeding the nutlets by 0.5–0.7 mm.

DISTRIBUTION: Iran, Afghanistan, West Pakistan, Kashmir, Turkestan, Pamir Alaj, Kara Kum, Kizil Kum, Syr Darya, Caspian Arals, Dsungaro-Tarbagatai, Tien shan.

West Pakistan: GILGIT AGENCY: Karakorum range, Baltistan, upper end of Hushe Valley, Chandakore glacier basin at the foot of the Masherbrum, Shahircho, 3600 m., *Webster & Nasir 5974* (GH-mixed with *R. leiocarpa*); Dirran, upper branch of Bagrot Valley, *Conway 332* (K); Hunza Valley, Zangia Harar, 4000 m., *Russell 1068* (BM).

Kashmir: Zanskar, Kargia, 4500 m., *Koelz 5582* (GH, MICH, US).

Rochelia incana Kar. & Kir. sensu Bunge (in Reliq. Lehmann. 243. 1851; Mém. Acad. Sci. St. Pétersb. Savants Étr. 7: 412. 1852; Boiss. Fl. Orient. 4: 244. 1875) is a misidentification.

8. **R. laxa** I. M. Johnston, Jour. Arnold Arb. 21: 55. 1940.

TYPE: Kashmir: Zanskar, Bok, 3450 m., camp ground, Sept. 13, 1931, *Walter Koelz 2946a* (GH-holotype), *2946b* (GH-isotype).

Annual, erect herb to 20 cm. tall with much branched roots. Stem usually branched near the base, branches long, divaricate; stem and branches covered with thin, erect to suberect, white trichomes, on the lower parts usually arising from white tuberculate bases. Basal leaves ovate, obovate or oblanceolate, obtuse to roundish at apices, entire, attenuated towards the bases, 5–20 mm. long, 3–5 mm. broad, both surfaces covered with short, thin, white trichomes arising from white tuberculate bases; middle cauline leaves longer; upper cauline leaves shorter and narrower, covered more densely with comparatively longer, thicker trichomes. Inflorescence lax, unilateral, bracteate, bracts minute, ovate-lanceolate. Pedicels in flower lacking to 0.5 mm. long, in fruit to 8 mm. long, narrowed towards the base, covered with spreading, uncinate trichomes. Calyx divided nearly to the base, lobes in flower 1 mm. long, lanceolate, densely pubescent, in fruit oblong-lanceolate, erect to deflexed, 2.5–4 mm. long, 0.5–0.8 mm. broad, usually shorter or sometimes equalling the nutlets, rarely exceeding them by 0.5–1 mm., covered with white, uncinate trichomes, arising from conspicuous tuberculate bases. Corolla blue, ca. 2 mm. long, tubular, tube equalling the calyx, lobes ovate, suberect, 0.5 mm. long. Nutlets 2, white, erect or slightly tilted, tuberculate, 3–3.3 mm. long. Style exceeding the nutlets by 0.2–0.5 mm.

DISTRIBUTION: West Pakistan, Kashmir, northwest India.

West Pakistan: CHITRAL STATE: Lutko, 2550 m., *Bowes Lyon 789* (BM). GILGIT AGENCY: Baltistan, Marpu Nullah, 3600–4000 m., *Duthie 11839* (K); Naltar, 3300 m., *R. R. Stewart 26336, 26339* (BM).

Kashmir: Mitsahoi, Ladak Road, 3150 m., *R. R. Stewart 10002a* (GH); Rach-

ogba, Rupshu, 4020 m., *Koelz 2104* (GH); Bok, Zanskar, 3450 m., *Koelz 2946a, 2946b* (GH-type).

I. M. Johnston (l. c.) considered *Rochelia laxa* closely related to *R. macrocalyx* and distinguished it from the former species by its much more loosely branched habit, elongate inflorescence, deflexed spreading rather than ascending pedicels, and its coarser obtusish calyx lobes, which only slightly exceed the nutlets. *Rochelia laxa* appears to me to be very closely related to *R. peduncularis* rather than to *R. macrocalyx*. *Rochelia macrocalyx* is unique among all the species of the genus in having unguiculate sepals, each with a very strong midrib. The calyx of *R. laxa* is quite different and resembles very much that of *R. peduncularis* in its non-unguiculate, lanceolate and erect calyx lobes. From *R. peduncularis* it differs in pedicels lacking or to only 0.5 mm. long in flower and much shorter in fruit, at the minimum not twice the length of the calyx. Calyx lobes in *R. laxa* at the fruiting stage are 2.5–4 mm. long, while in *R. peduncularis* they are 4–6 mm. long. In the former species the calyx lobes hardly exceed the nutlets in length, while in the latter they usually exceed the nutlets by 2–4 mm.

19. **Asperugo** L. Sp. Pl. 198. 1753; Gen. Pl. ed. 5. 67. 1754.

TYPE SPECIES: *A. procumbens* L.

Annual procumbent herb. Flowers small, axillary, subsessile, solitary or in pairs. Calyx in flower divided to the base, much enlarged in fruit, lobes joined below the middle, compressed. Corolla blue, subcylindrical; faucal appendages distinct, semiorbicular. Stamens included. Gynobase columnar, with 4 elevations. Style short. Nutlets 4, ovoid, strongly flattened with the small circular areola above the middle and clearly to one side of the medial line.

One species, European, widely disseminated as a weed.

A. procumbens L. Sp. Pl. 138. 1753; DC. Prodr. 10: 146. 1846; Boiss. Fl. Orient. 4: 275. 1875; C. B. Clarke in Hook. f. Fl. Brit. India 4: 167. 1883; Brand, Pflanzenr. IV. 252 (Heft 97): 23. 1931; M. Pop. Fl. URSS 19: 530. 1953; Riedl in Rechinger, Fl. Iranica 48: 96. 1967.

TYPE: Habitat in Europae *ruderatis pinguibus*, Herb. No. 189.1 (LINN).

ICON.: Reichenb. Icon. Fl. Germ. 18: *t. 126*. 1858; Brand, l. c. *fig. 1*, M–P. 1931.

Annual, procumbent herb. Stems many, to 60 cm. long, flaccid, branched; stem and branches with short, stout, retrorse spinules. Leaves very variable, oblong-lanceolate to oblong-ovate, obtuse to acutish, usually attenuated into a short petiole towards the base, 30–60(–100) mm. long, 5–10(35) mm. broad, covered on both surfaces densely or sparsely with short, subappressed to subpatent, white trichomes, arising from minute

tuberculate bases. Flowers small, subsessile, solitary or in pairs. Pedicels in fruit 2–7 mm. long, usually reflexed. Calyx divided nearly to the base in flower, ca. 1.5 mm. long, enlarged in fruit to 15 mm., lobes joined below the middle, with few scattered spinules on the outside, glabrous inside. Corolla blue, 1.5–2 mm. long, lobes rounded, suberect; faucal appendages whitish. Nutlets ovoid, compressed, brownish, minutely verruculose, ca. 2.5 mm. long.

DISTRIBUTION: Asia and Europe.

West Pakistan: ATTOCK DIST.: Campbellpore, *Iftakhar s.n.* (PEU). CHITRAL STATE: Brumboret Gol, 2000 m., *Bowes Lyon 650* (BM); Ziarat, Lowari Pass, 2400 m., *Stainton 2340* (BM). GILGIT AGENCY: Shingo Valley, *Duthie s.n.* (E); KOHAT DIST.: 4 miles from Kohat, on Kohat-Bannu Road, *Kazmi s.n.* (PES). KURRAM AGENCY: near check post, between Tal and Parachinar, *Kazmi 203a* (PES). PESHAWAR DIST.: Between Mardan and Charsadda, *Kazmi 482a* (PES). QUETTA DIST.: Quetta, Sariab Road, 5 km. from Quetta, 1700 m., *Kazmi 1443* (PES); *Lamond 899* (E); *Rechinger 28823* (W); Peshin, 1700 m., *Lace 3472* (E); Quetta, *Lace 3465* (E); *A. H. Khan s.n.* (PFI–M); *Kazmi s.n.* (PES); Ziarat, *Jafri & Akbar 2128* (E); *M. A. Siddiqui 2020* (RAW); Sandeman Tangi, 2 miles from Ziarat, *Kazmi 1666a* (PES). SWAT STATE: Mingora, *Kazmi 432b* (PES). Reported from: North Waziristan: Dariawarti, *Blatter & Fernandes s.n.*

Kashmir: Chinari, *Kazmi 526a* (PES); Muzzaffarabad, near the bridge, *Kazmi s.n.* (PES); Purig, Tangola, *Koelz 6090* (US). Reported from: Poonch, *R. R. Stewart s.n.*; Murpur, *R. R. Stewart s.n.*

20. **Omphalodes** Moench, Meth. 419. 1794.

TYPE SPECIES: *O. linifolia* (L.) Moench.

Annual or perennial strigose or villous herbs. Leaves alternate or sometimes the lower opposite. Inflorescence of simple or branched racemes. Calyx divided to the base. Corolla funnelform, campanulate or salverform, lobes patent; faucal appendages, distinct, semilunar. Anthers ovate, included; filaments short. Nutlets depressed-spherical to ovoid, externally umbilicate, dentate to glochidiate, margins usually incurved, attached longitudinally to and exceeding the gynobase.

Species about 24, distributed in Eurasia and Mexico.

O. heterophylla Rech. f. & H. Riedl in Oesterr. Bot. Zeitschr. **110**: 532. 1963; Riedl in Rechinger, Fl. Iranica **48**: 98. 1967.

TYPE: West Pakistan: Swat: Himalaya bor. occid. Kalam, ca. 35° 30′ N, 72° 30′ E, Substr. granite, ca. 2200 m., 22. 8. 1962, *K. H. Rechinger 19442* (W-holotype).

Perennial, tufted, prostrate to rarely ascending herb. Stems numerous, simple to much branched, covered with white spreading trichomes, 7–35 cm. long. Basal leaves lanceolate, petiolate, petioles nearly 10 mm. long,

lamina 30–55 mm. long, 9–18 mm. broad, acute, one nerved, covered on both surfaces with rigid, appressed, white trichomes, arising from distinct tuberculate bases; cauline leaves much smaller than the basal leaves, oblong to oblong-lanceolate, sessile to shortly petiolate, 10–25 mm. long, 3–8 mm. broad; upper cauline leaves, sessile, auriculate. Inflorescence lax, short in flower, elongated in fruit, bracteate, lower bracts 10–18 mm. long, acute, the upper ones 2–10 mm. long, lanceolate, indistinct in the uppermost flowers. Pedicels 2–4 mm. long in flower, recurved, 4–9 mm. long, in fruit. Calyx divided to the base, lobes 2–2.5 mm. long in flower, to 4 mm. long in fruit, patent, incurved at apex. Corolla campanulate, blue, 3 mm. long, slightly exceeding the calyx, corolla tube equalling or slightly shorter than the calyx, lobes suborbicular, patent, 1–1.5 mm. long, faucal appendages much broader than long, incurved. Anthers minute, filaments scarcely distinct, inserted at the middle of the corolla tube. Style 1–1.5(–2) mm. long, stigma capitate or indistinctly bifid. Nutlets ovoid, subacute, 2 mm. long, margins swollen, dorsal face more or less plane, sparsely tuberculate-aculeate, ventrally densely tuberculate, carinate below and sometimes also above the areola, areola orbicular at base, narrow at apex, covering ⅔ length of the nutlet ventrally. Gynobase short, narrow, conical.

DISTRIBUTION: West Pakistan.

West Pakistan: CHITRAL STATE: Drosh, Beorai, 4000 m., *Bowes Lyon 198* (BM, E). SWAT STATE: Kalam, 2200 m., *Rechinger 19442* (W-type).

21. **Paracaryum** (DC.) Boiss. Diagn. Pl. Orient. **11**: 128. 1849.

Omphalodes Moench, Sect. *Paracaryum* DC. Prodr. **10**: 159. 1846.
Omphalodes Moench, Sect. *Mathia* DC. Prodr. **10**: 169. 1846, *pro parte*.

TYPE SPECIES: *P. rugulosum* (A.DC.) Boiss. (lectotype species).

Annual, biennial or perennial, erect, decumbent or prostrate herbs. Basal leaves many, usually with long petioles; cauline leaves usually sessile. Inflorescence short in flower, later elongated, ebracteate to bearing several bracts. Calyx divided to the base, lobes more or less enlarged in fruit. Corolla blue to various shades of purple-brown, infundibuliform, subcampanulate or cylindrical, lobes usually short; faucal appendages present. Anthers usually included, rarely with exserted apices, elliptical to linear; filaments distinct. Style usually shorter than the calyx; stigma capitate. Nutlets 4, dorsal middle area smooth, aculeolate or glochidiate, often carinate, margins winged, wings inflexed, entire to lacerate, bearing glochidia, membranous, attached ventrally throughout their length to the narrow, conical gynobase.

Species about 15, distributed from northeast Africa to south and southeast Russia, Arabia, Iran, Afghanistan, West Pakistan, Kashmir and northwest India.

KEY TO THE SPECIES

a. Species perennial; nutlets 5–7 mm. long.
  b. Nutlets 5 mm. long; pedicels in fruit ca. 4 mm. long; calyx lobes 4 mm. long, linear-oblong, not enlarged in fruit; corolla cylindrical-campanulate. ..... 1. *P. rugulosum.*
  b. Nutlets 6–7 mm. long; pedicels 7–12 mm. long in fruit; calyx lobes ca. 4 mm. long in flower, enlarged in fruit to 6 mm., lanceolate; corolla infundibuliform. ..... 2. *P. platycalyx.*
a. Species annual; nutlets 2.5–4(–5) mm. long.
  c. Nutlets ovoid, 4–5 mm. long; basal leaves distinctly petiolate. ..... 3. *P. calathicarpum.*
  c. Nutlets round, 2.5–4 mm. in diameter; basal leaves indistinctly petiolate. ..... 4. *P. intermedium.*

1. **P. rugulosum** (DC.) Boiss. Diagn. Pl. Orient. **11**: 129. 1848; Fl. Orient. **4**: 256. 1875; Aitch. Bot. Afgh. Delim. Comm. 89. 1888; Brand, Pflanzenr. IV. 252 (Heft 78): 48. 1921; Riedl in Rechinger, Fl. Iranica **48**: 99. 1967.

Omphalodes rugulosa DC. Prodr. **10**: 160. 1848.
Paracaryum rubriflorum Stocks in Jour. Bot. Hook. **4**: 175. 1852.

TYPE: In monte Horeb Arabiae Petreae, *Aucher s.n.* (G).

ICON.: Brand, l. c. *fig. 5, A-F.* 1921.

Perennial, erect herb, 10–40 cm. tall. Stems solitary or few, branched, branches long; stems and branches densely covered with thick, usually retrorse, subpatent, white to grayish trichomes to 2 mm. long, arising from tuberculate bases. Basal and some of the lower cauline leaves petiolate, linear-lanceolate to oblong-lanceolate, acute, margins entire, (including petioles) 40–170 mm. long, 2–15 mm. broad, densely covered on both surfaces with trichomes like those of the stem; cauline leaves sessile, shorter and narrower. Pedicels to 2 mm. long in flower, to 6 mm. long, densely pubescent, recurved in fruit. Calyx divided to the base, lobes in flower ca. 4 mm. long and 1 mm. broad, oblong, densely pubescent with retrorse, subpatent trichomes, to 5 mm. long and 2 mm. broad in fruit, ovate to ovate-lanceolate, acutish, subpatent, rarely reflexed. Corolla purple-violet to bluish-violet, cylindrical-campanulate, 4–5 mm. long, tube more or less equalling the limbs, limbs divided to the middle into more or less patent lobes; faucal appendages present. Style 2–3 mm. long. Nutlets to 6 mm. long and 5 mm. broad, ovate, broadly winged at the margins, wings incurved, rugulose, irregularly dentate on the inner margin, dorsally sometimes tuberculate; dorsal middle area smooth or bearing few vertical appendages, appendages at apex glochidiate.

DISTRIBUTION: Egypt, Arabia, Iran, West Pakistan.

West Pakistan: QUETTA DIST.: Quetta, *Dick-Peddie 315* (MICH); Gwal, 2000 m., 24. 4. 1888, *Lace s.n.* (E); Zarghun, 2200 m., *Lace 3731* (E). Miscellaneous: Baluchistan, Herb. Ind. Or. Hook. f. & Thoms., *Stocks s.n.* (GH-isotype of *P. rubriflorum* Stocks). Reported from: Quetta, Khanozai, *Duthie (?) 18924* (DD).

2. **P. platycalyx** Riedl, Oesterr. Bot. Zeitschr. 110: 535. 1963; in Køie & Rechinger, Biol. Skr. 13(4): 205. 1963; in Rechinger, Fl. Iranica 48: 102. 1967.

TYPE: Afghanistan: Herat, Jija, 900 m., *Køie 4404* (w-holotype, c-isotype).

ICON.: Riedl, l. c. *fig. 156.* 1963.

Perennial, erect to ascendent, 15–25 cm. tall. Stems many, branched, covered densely with up to 2 mm. long, thick, patent, white trichomes arising from minute tuberculate bases. Basal leaves petiolate, (including petioles) 70–130 mm. long, 7–10 mm. broad, petioles usually longer than the lamina, lamina lanceolate, tapering at both ends, acutish, margins plane, covered on both surfaces with subpatent, more or less retrorse trichomes, like those of the stem; cauline leaves sessile, sometimes more or less semiamplexicaul, gradually reduced in size upwards. Pedicels 2 mm. long in flower, to 12 mm. long in fruit, more or less recurved. Calyx divided to the base, lobes oblong-ovate, densely hairy, in flower ca. 4 mm. long, 1 mm. broad, enlarged in fruit to 6.5 mm. long and 2.5 mm. broad, lanceolate, spreading. Corolla blue to purplish-blue, infundibuliform, 6–7 (–8) mm. long, tube longer than limb, lobes broad, rounded; faucal appendages broader than long. Style 2–3 mm. long. Nutlets up to 6(–7) mm. long, 5–6 mm. broad, ovate, broadly winged at the margins, wings incurved, rugulose, irregularly dentate on the inner margins, middle dorsal area indistinctly carinate, smooth or bearing few vertical appendages, appendages glochidiate at their apices.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: KALAT STATE: Surab to Kalat, ca. 20 km. from Surab, 1800 m., *Kazmi 1312a* (PES); *Lamond 669* (E); *Rechinger 28345* (W). QUETTA DIST.: circa 50 km. from Quetta, Chiltan, between Dulai and Kanak, 1600 m., *Kazmi 1549* (GH, PES); *Lamond 1093* (E); *Rechinger 29118* (W, G); Bolan Pass, south of Quetta, 1500 m., *Kazmi 1397a* (PES); *Lamond 883* (E); *Rechinger 28795* (W).

Paracaryum platycalyx is very closely related to *P. rugulosum* in the form of its leaves, flowering parts, and nutlets and can only be differentiated from the former species by its larger nutlets, pedicels longer in fruit, and the slightly longer fruiting calyx lobes.

With the little material from our area available for study, the differences between the two species appear only in the dimensions of pedicels, calyx lobes, and nutlets, and not in their shape or structure. It is possible that on examining more material *Paracaryum platycalyx* may prove to be only a variation of *P. rugulosum*.

3. **P. calathicarpum** (Stocks) Boiss. Fl. Orient. 4: 254. 1875; Brand, Pflanzenr. IV. 252 (Heft 78): 48. 1921; Riedl in Rechinger, Fl. Iranica 48: 104. 1967.

Echinospermum calathicarpum Stocks in Jour. Bot. Hook. 4: 175. 1852.

TYPE: *Baluchistan superior, Stocks 1003* (K-holotype, G-isotype).

ICON.: Riedl in Køie & Rechinger, Biol. Skr. 13(4): 204. *fig. 154, 155.* 1963; in Rechinger, Fl. Iranica, l. c. *t. 19. fig. 2.* 1967.

Annual, erect, up to 25 cm. tall. Stem usually solitary, much branched, branches long, divaricate; stem and branches covered with thin, crisped, subappressed, antrorse trichomes, to 0.5 mm. long, arising from minute tuberculate bases. Basal leaves oblong-spathulate, petiolate, (including petioles) to 50 mm. long and 8–10 mm. broad, apices obtuse to roundish, gradually narrowed towards the base into a short petiole, loosely covered on both surfaces with very short, crisped, patent to subappressed white trichomes, arising from large tuberculate bases; lower cauline leaves very short petiolate, the upper sessile, gradually reduced in size. Pedicels in flower lacking to 0.5 mm. long, in fruit to 4 mm. long, stout, pubescent, more or less reflexed. Calyx divided to the base, lobes oblong, acute, pubescent, 1–1.5 mm. long in flower, enlarged in fruit to 2.5–3 mm. long, spreading. Corolla blue, campanulate, 1.5–2 mm. long, limb shorter than the tube, lobes minute. Style ca. 0.5 mm. long, pubescent. Nutlets ovoid, 4–5 mm. long, 3.5–4 mm. broad, margins broadly winged, wings inflexed, laterally blistered, blisters in many rows, those of the outer row slightly elongate to partly mammillate, dorsally rugulose, tuberculate, inner margins irregularly dentate, middle dorsal area tuberculate to vertically appendiculate, appendages glochidiate at apex; one pair of opposite nutlets usually with narrower marginal wings.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: MAKRAN DIST.: 70 km. northeast of Panjgur, 1100 m., *Kazmi 1271b* (PES); *Rechinger 28221* (W); Nag, between Panjgur and Surab, 1300 m., *Kazmi 1278a* (PES); *Lamond 632* (E); *Rechinger 28260a* (G, W). QUETTA DIST.: 20 km. west of Quetta, *Kazmi 1589b* (PES); *Rechinger 29081* (W). Miscellaneous: Baluchistan superior, *Stocks 1003* (K). Reported from: Quetta, inter Zhob et Sambaza, 26 km. north of Fort Sandeman versus Wana, 1500 m., *Rechinger 24844* (W); infra Mach versus Ab-e-Gum, *Rechinger 28484* (W); Panjgur, 1000 m., *Rechinger 28177*(W).

4. **P. intermedium** (Fresen.) Lipsky, Acta Horti Petrop. 26(2): 487. 1910; Brand, Pflanzenr. IV. 252 (Heft 78): 47. 1921; M. Pop. Fl. URSS 19: 602. 1953; Riedl in Rechinger, Fl. Iranica 48: 105. 1967.

Cynoglossum intermedium Fresen. in Mus. Senckenb. 1: 169. 1834.
Omphalodes intermedia Decne. Ann. Sci. Nat. Paris 2: 255, 256. 1834.
Paracaryum micranthum (DC.) Boiss. Diagn. Pl. Orient. 11: 129. 1849; Fl. Orient. 4: 255. 1875.
Omphalodes micrantha DC. Prodr. 10: 159. 1846.

TYPE: not indicated.

ICON.: Riedl, l. c. 48: *t. 19. fig. 4.* 1967.

Annual, erect to ascending herb, 5–30 cm. tall. Stems solitary to many, branched near the base, branches long, delicate, more or less spreading,

covered with crisped patent to subappressed white trichomes to 0.5 mm. long, arising from minute tuberculate bases. Basal leaves usually obtuse sometimes acutish, entire, 20–40 mm. long, 3–6 mm. broad, attenuated towards the base into a very short to indistinct petiole, covered on both surfaces with thick, patent, white trichomes to 1 mm. long, arising from large, white, tuberculate bases; cauline leaves sessile, linear-oblong, gradually reduced in size upwards. Inflorescence long, lax, usually bracteate in the lower part, bracts 1–2. Pedicels very short in flower, elongated to 15 mm. in fruit, pubescent, suberect to horizontal or sometimes reflexed. Calyx divided nearly to the base, lobes 1–1.5 mm. long in flower, 2–3.5 mm. long in fruit, linear to oblong-ovate, obtuse to acute. Corolla blue, campanulate to cylindric-campanulate, 1.5–2.5 mm. long, limbs subequal to little shorter than the tube; faucal appendages semilunar to subquadrate. Anthers attached to the middle of the corolla tube. Nutlets roundish, 2.5–4 mm. in diameter, broadly winged at the margins, wings inflexed, leaving a small to large aperture in the middle, more or less longitudinally rugulose, sometimes with few tubercles or densely minutely papillate, inner margin forming the aperture lobed, irregularly dentate or pubescent, middle dorsal area aculeate or vertically appendiculate, appendages glochidiate.

DISTRIBUTION OF SPECIES: Egypt, Arabia, Iran, Afghanistan, West Pakistan, Caspian Aral, Pamir Alaj, Kizil Kum, Tien Shan.

KEY TO THE VARIETIES

a. Inflexed marginal wings of the nutlets densely white papillate on the upper surface. ..... 4c. var. *papillosum*.
a. Inflexed marginal wings of the nutlets glabrous or rarely inconspicuously papillate.
  b. Aperture formed by the inflexed marginal wings of the nutlets very small, stellate. ..... 4b. var. *stellatum*.
  b. Aperture formed by the inflexed marginal wings of the nutlets large, roundish. ..... 4a. var. *intermedium*.

4a. Var. intermedium.

Basal leaves linear-spathulate; cauline leaves linear-oblong, obtuse. Pedicels 5–15 mm. long in fruit. Calyx lobes oblong-ovate. Corolla campanulate, limb subequalling the corolla tube. Inflexed marginal wings of the nutlets dorsally glabrous, rarely indistinctly minutely papillose; margin forming the central aperture subentire to irregularly dentate or lobed.

DISTRIBUTION OF VAR.: as that of species.

West Pakistan: QUETTA DIST.: 8 miles northwest of Harnai, 900–1200 m., *Kazmi 1645b* (PES); *Rechinger 29556* (W); near Ziarat, 2400 m., *Kazmi 1656b* (PES); *Jafri & Akbar 2145* (BM, E). Miscellaneous: Baluchistan, Herb. Ind. Or. Hook. f. & Thoms., *Stocks s.n.* (GH–as *Omphalodes micrantha*). Reported from:

South Waziristan, Tank, *Williams*; Quetta, Wam Tangi, 1500 m., *Munro*; Fort Sandeman, 1500 m., in Herb. Dehra Dun; Shinger, 50 km., N. Fort Sandeman, 2000 m., *Rechinger 29898* (W); 38 km. E. Gumbaz, 1000 m., *Rechinger 29695* (W); KALAT STATE: Inter Kolpur et Mach, 900–1800 m., *Rechinger 28432, 28437* (W).

4b. Var. **stellatum** (H. Riedl) Kazmi, comb. nov.

Paracaryum stellatum H. Riedl in Rechinger, Fl. Iranica **48**: 104. 1967.

TYPE: West Pakistan: Kalat, inter Kolpur et Mach. 900 m., *K. H. Rechinger 28434* (W).

ICON.: Riedl, l. c. **48**: *t. 19. fig. 3.* 1967.

Basal leaves oblong to linear-oblong; cauline leaves linear to linear-lanceolate, acutish. Pedicels to 6 mm. long in fruit. Calyx lobes linear, acutish. Corolla campanulate, limbs subequal to the corolla tube. Inflexed margin of the nutlets, dorsally glabrous or rarely indistinctly papillose, margin forming the central aperture dentate, teeth triangular, central aperture stellate.

DISTRIBUTION OF VAR.: West Pakistan, Afghanistan.

West Pakistan: KALAT STATE: between Kolpur and Mach, 900 m., *Rechinger 28438* (W-holotype); *Kazmi 1331d* (PES). QUETTA DIST.: Inter Qila Abdullah et Sheila Bagh, 1600–1900 m., *Rechinger 29033* (W); Saranan, 8–9 miles north of Quetta, *Kazmi 1501a* (PES); Spin Karez, *Kazmi 1615b* (PES).

4c. Var. **papillosum** (DC.) Kazmi, comb. nov.

Omphalodes papillosa DC. Prodr. **10**: 159. 1846.
Paracaryum papillosum (DC.) Gürke in Engl. & Prantl. Nat. Pflanzenfam. IV. **3a**: 105. 1893; Riedl in Rechinger, Fl. Iranica **48**: 105. 1967.

TYPE: Ad montem Sinai, *Schimper 123* (G–holotype, GH–isotype).

Basal leaves oblong to linear-oblong; cauline leaves linear to linear-lanceolate, acutish. Pedicels to 10 mm. long in fruit. Calyx lobes more or less linear, acutish. Corolla cylindrical-campanulate, broad at the mouth, limb much shorter than the corolla tube. Inflexed marginal wings of the nutlets dorsally densely and minutely papillose, forming the central aperture at the margins, subentire, lobed or irregularly dentate, aperture broad.

DISTRIBUTION OF VAR.: as that of species.

West Pakistan: MAKRAN DIST.: Near Nag, *Kazmi 1258b* (PES). QUETTA DIST.: between Wam Tangi and Akhtari, *Kazmi 1763* (PES); Wam Tangi, *Munro s.n.* (K); Harnai, *Lace 2699* (G); Ziarat, *Santapau 6452* (GH). Reported from: Inter Kolpur and Mach, *Rechinger 28433.*

Paracaryum intermedium is very variable in the form of its leaves, in the length of pedicels, and in the margin and surface of the inflexed wings of the nutlets. Because the distinguishing characters are not very constant

and since intermediate forms are found, I consider *P. stellatum* and *P. papillosum* only variations of *P. intermedium*.

22. **Mattiastrum** (Boiss.) Brand, Repert. Sp. Nov. **14**: 150. 1915.

Paracaryum Boiss. Sect. 2. *Mattiastrum* Boiss. Diagn. Pl. Orient. **11**: 130. 1849.

TYPE SPECIES: not indicated.

Usually perennial or biennial, rarely annual herbs. Inflorescence terminal to axillary, ebracteate or rarely bearing 1–2 bracts. Calyx usually divided to the base, lobes 5, not at all to slightly enlarged in fruit. Corolla subcylindrical, to infundibuliform or hypocrateriform, limb obviously distinct from the corolla tube, faucal appendages 5, conspicuously developed inside the corolla throat. Anthers included. Nutlets usually winged at the margins, sometimes the wings of the pair of two opposite nutlets reduced, wings plane, to rarely slightly incurved, never inflexed as in *Paracaryum*, middle dorsal area not covered by the wings, wings dentate to appendiculate at the margins, appendages glochidiate, nutlets attached throughout their length to the narrow columnar gynobase.

Species about 30, distributed in southwestern Asia.

KEY TO THE SPECIES

a. Calyx lobes 3–5 mm. long in flower; corolla 10–12 mm. long. ..... 1. *M. asperum*.
a. Calyx lobes 1–2 mm. long in flower; corolla 2–4 mm. long.
  b. Basal leaves (including petioles) 100–140 mm. long, 30–45 mm. broad, ovate to oblong-ovate. ..... 4. *M. thomsoni*.
  b. Basal leaves (including petioles) to 90 mm. long and 15 mm. broad, oblong-lanceolate to oblong-spathulate.
    c. Nutlets 5–8 mm. long.
      d. Plants spreading pubescent; pedicels to 1 mm. long in flower, to 6(–8) mm. long in fruit, slender; corolla blue; style 1.5–2 mm. long. ..... 3. *M. howardii*.
      d. Plants appressed pubescent; pedicels lacking in flower, in fruit to 2 mm. long, thick; corolla bluish-white to pink; style 0.5–1 mm. long. ..... 2. *M. himalayensis*.
    c. Nutlets 2–4 mm. long.
      e. Plants erect to ascendent; stem stout, thick; basal leaves many; marginal wings of the nutlets plane at the edges, dentate, teeth blunt not glochidiate at apex. ..... 5. *M. tibeticum*.
      e. Plants erect to prostrate, stem weak, slender; basal leaves 1–2 or missing; marginal wings of the nutlets recurved at the edges, dentate, teeth produced, glochidiate at apex. ..... 6. *M. bungei*.

1. **M. asperum** (Stocks) Brand, Repert. Sp. Nov. **14**: 153. 1915; Pflanzenr. IV. 252 (Heft 78): 61. 1921; Riedl in Rechinger, Fl. Iranica **48**: 114. 1967.

Paracaryum asperum Stocks in Jour. Bot. Hook. **4**: 175. 1852; Boiss. Fl. Orient. **4**: 261. 1875.

Mattiastrum honigbergeri Rech. f. Ann. Naturh. Mus. Wien **55**: 14. 1947; Riedl in Rechinger, Fl. Iranica **48**: 114. 1967, *syn. nov.*

TYPE: Baluchistan superior, *Stocks 906* (K).

ICON.: Riedl in Køie & Rechinger, Biol. Skr. 13(4): 213. *fig. 164*. 1963 (under *M. honigbergeri*).

Shrubby perennial, 20–60 cm. tall. Stems many, branched, branches long; stem and branches covered with crisped, patent, thick, white trichomes to 2 mm. long, arising from tuberculate bases. Basal leaves petiolate, (including petioles) to 100 mm. long, 12 mm. broad, oblong-ovate, obtuse, attenuated towards the base, both surfaces covered densely with short trichomes to 1 mm. long intermixed with thick trichomes to 2.5 mm. long, all arising from prominent tuberculate bases and more or less spreading; middle cauline leaves linear-oblong, sessile, little shorter than the basal ones; upper cauline leaves much shorter and narrower. Inflorescence terminal or axillary, lax, much elongated in fruit. Pedicels 1–2 mm. long in flower, elongated to 6 mm. in fruit, usually erect or sometimes reflexed. Calyx divided to the base, lobes linear-oblong, acute, densely pubescent, 3–4(–5) mm. long in flower, slightly enlarged in fruit. Corolla purple-violet to blue, cylindrical-infundibuliform, 6–12 mm. long, limb more or less equalling the corolla tube, lobes short; faucal appendages semilunar. Nutlets (6–)8–10 mm. in diameter, broadly winged at the margins, wings dentate, teeth triangular, usually glochidiate at apex, dorsal middle area vertically appendiculate, appendages glochidiate.

DISTRIBUTION: West Pakistan, Afghanistan.

West Pakistan: QUETTA DIST.: Urak, 2000 m., *Santapau 6731* (GH); *R. R. Stewart 691* (MICH); Ziarat, Sandeman Tangi, 2 miles from Ziarat, 2500 m., *Kazmi 1660* (PES); Quetta to Ziarat at top of Pass, 2500 m., *Lamond 1868* (E); *Rechinger 29056* (W); Ziarat, Swiss Zool. Mission (May, 1953), *s.n.* (BM); between Qila Abdullah and Sheila Bagh, *Kazmi 1533* (PES); Quetta to Chaman, Khojak Pass, above Sheila Bagh, 2000–2300 m., *Lamond 1068* (E); *Rechinger 29056* (W); Ziarat, *Santapau 6435* (GH). Miscellaneous: Baluchistan, in Herb. Ind. Or. Hook. f. & Thoms., *Stocks s.n.* (GH–probable duplicate of *Stocks 906*). Reported from: Quetta, Tak, *Rechinger 28402* (W); Gwal versus Surkh, Kakar in valley Lora, *Lace s.n.*; Chiltan inter Dulai et Kanak, 1600 m., *Rechinger 29119* (W); Gwoshki, 2100–2400 m., *Munro*(?); Kawas Tangi, 1800 m., *Munro*(?); Zarghun, 1500 m., *Lace 3731* in part (E).

The only distinguishing character cited between *Mattiastrum asperum* and *M. honigbergeri* is the length of corolla which, in the former species is said to be 10 to 12 mm. and in the latter 6 to 8 mm. The specimens I examined, show a variation in the length of corolla between 6 to 12 mm. and *M. honigbergeri* represents the variation with shorter corollas.

2. **M. himalayense** (Klotzsch) Brand, Repert. Sp. Nov. **14**: 156. 1916;

Pflanzenr. IV. 252 (Heft 78): 65. 1921; Riedl in Rechinger, Fl. Iranica 48: 116. 1967.

Mattia himalayensis Klotzsch in Bot. Ergebn. Reis. Prinz Waldemar Bot. 94. *t. 64.* 1862.

Paracaryum himalayense (Klotzsch) C. B. Clarke in Hook. f. Fl. Brit. India 4: 161. 1883; Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. 3a: 105. *fig. 42, L–O* 1893; M. Pop. in Fl. URSS 19: 597. 1953.

TYPE: Himalaya, *Hoffmeister s.n.* (HEID).

ICON.: Riedl in Køie & Rechinger, Biol. Skr. 13(4): 212. *fig. 162, 163.* 1963; Klotzsch, l. c. *t. 64.* 1862; Gürke, l. c. *fig. 42, L–O.* 1893; Brand, l. c. *fig. 10, L–O.* 1921; M. Pop. l. c. *t. 30. fig. 1.* 1953.

Biennial to perennial, erect, to 60 cm. tall. Stems solitary to many, branched, branches long, more or less divaricate; stem and branches densely covered with subpatent to subappressed white trichomes 0.5–1 mm. long, not arising from tuberculate bases, sometimes intermixed with thicker trichomes to 1 mm. long, arising from prominent tuberculate bases. Basal leaves (including petioles) 50–90 mm. long, 5–15 mm. broad, oblong, oblong-lanceolate or lance-spathulate, obtuse, margins sometimes slightly revolute, densely covered on both surfaces with variable, very thin to quite thick, appressed to subpatent, white trichomes 0.5–1 mm. long, arising from tuberculate bases or not; cauline leaves sessile, lanceolate, much reduced in size. Inflorescence terminal and axillary, much contracted in flower, elongated in fruit, lax. Pedicel absent in flower, in fruit stout, hairy, erect or horizontal, rarely reflexed, usually 1–2 mm. long. Calyx divided nearly to the base, in flower 1.5–2 mm. long, in fruit elongated to 3 mm., ovate to oblong, obtuse, hairy. Corolla bluish-white to pink, 2–4 mm. long, cylindric-campanulate, tube slightly longer than the limb; faucal appendages trapeziform. Nutlets suborbicular, 5–7(–8) mm. in diameter, marginal wings broad, plane or slightly curved at the bluish, broadly dentate margins, teeth triangular, bearing glochidia at apex. Stigma 0.5–1 mm. long.

DISTRIBUTION OF SPECIES: Afghanistan, Pamir Alaj, West Pakistan, Kashmir, northwest India.

2a. Var. himalayense

Plants biennial; stem solitary, slender, less branched, branches not much spreading.

West Pakistan: GILGIT AGENCY: Baltistan, Chorbat, 3000 m., *Hunter-Winston 10246* (K). Miscellaneous: Himalaya, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (K–as *Omphalodes* no. 4).

Kashmir: Reported from: Ladak, 4600 m., *Meebold 4236.*

2b. Var. fallax (Rech. f. & H. Riedl) Kazmi, comb. nov.

Mattiastrum himalayense subsp. *fallax* Rech. f. & H. Riedl in Rechinger, Fl. Iranica 48: 117. 1967.

TYPE: Afghanistan: Bareki Chaidan, on the way to Band-e-Amir, 2800 m., *Hedge & Wendelbo 4719* (BG).

ICON.: Riedl, l. c. *t. 22*. 1967.

Plants perennial, stems many, stout, much branched, branches divaricate.

West Pakistan: GILGIT AGENCY: Baltistan: Shagarthang Valley, 3000 m., *Duthie 12, 140* (K).

Kashmir: ZASKAR: Seni, Phe, 3600 m., *Koelz 5821* (GH, MICH, US); Kargia, 4300 m., *Koelz 5470* (GH, MICH, US); LADAK: Rabila, *Koelz 6153* (MICH, US).

Riedl (l. c. 1967) recognized the perennial, many stemmed form as subspecies *fallax*, considering it to be confined to Afghanistan or possibly extending to Pamir Alaj and thus representing the western area of distribution of the species *Mattiastrum himalayense*. The specimens I examined show that this form extends to West Pakistan, Kashmir, and even to northwest India, [Kangra Dist.: Spiti Valley, Dankhar, 4000 m., *Bhagwan Singh 256* (MICH)] and covers the same area as the typical form. Therefore, I consider both taxa only varieties of *M. himalayense*. The diameter of the nutlets in variety *fallax* has been given by Riedl as 7 to 8 mm., which is so only rarely. Usually the nutlets are the same size in both varieties.

3. **M. howardii** [2] Kazmi, sp. nov.

TYPE: West Pakistan: Gilgit Agency, Dist. Astore, 7800 ft., 25. 7. 1892, *J. F. Duthie s.n.* (BM-holotype, E-isotype).

Herba annua vel biennis (?), erecta ad 35 cm. alta. Caulis plerumque solitarius, interdum 2–3, striatus, ramosus, rami ad 20 cm. longi, plus-minusve divaricati; caules ramique pilis albis patentibus rigidis, ad basim manifeste tuberculatis, vestiti. Folia basalia petiolata, ad 40–60 mm. longa (petiolis inclusis) et 5–10 mm. lata, oblongo-ovata, obtusa vel subrotundata ad apices, ad basim attenuata, supra infraque dense pilosa, pili tenues albi; petioli, praecipue ad margines, pilis ad 1.5 mm. longis; folia caulina media pauca, sessilia, lanceolata, acuta, basim apicemque attenuata, quam folia basalia angustiora brevioraque, pilis longioribus sparse vestita, pili ad basim tuberculati. Inflorescentia ad anthesin brevis, in fructu perelongata, laxa, interdum 1–2-bracteata. Pedicellus ad anthesin ± 1 mm. longus, hirsutus, in fructu perelongatus et usque ad 6(–8) mm. longus, tenuis, erectus, raro deflexus. Calyx ad basim divisus, lobi ad anthesin 1.5–2 mm. longi, oblongi, in fructu accrescentes ad 3–4 mm. longi et 1 mm. lati, erecti. Corolla caerulea, ca. 2 mm. longa, cylindrico-campanulata, tubus quam limbus longior, lobi 0.7–8 mm. longi, ovati; appendices faucales suborbiculares. Antherae 0.6 mm. longae, oblongae, ad medium tubi corollae insertae. Nuculae subrotundatae, 6–7 mm. diam. ad margines alatae, alae ca. 2 mm. latae, ad margines complanatae, late

[2] I am naming this species in honor of Professor Richard A. Howard, Director of the Arnold Arboretum of Harvard University.

dentatae, dentes ad apicem glochidiati; pars media dorsalis verticale appendiculata, appendices apice glochidiatae, paginae laterales ventralesque minute tuberculatae. Stylus 1.5–2 mm. longus.

DISTRIBUTION: West Pakistan.

West Pakistan: GILGIT AGENCY: Astore, 2500 m., *Duthie s.n.* (BM, E); Gurikot to Godai, on Gilgit road, 2650 m., *R. R. Stewart 18930* (GH); Gurikot to Das Kirini, 2500–2700 m., *R. R. Stewart 22979* (GH).

The new species, *Mattiastrum howardii*, is closely related to *Mattiastrum himalayense*, from which it differs in the loose, always spreading, uniform trichomes on the stem, branches, and leaves; in the subsessile to short (1 mm.) pedicellate flowers, the slender, erect or rarely slightly reflexed pedicels elongating to 6(–8) mm. in fruit; and the blue corolla with style 1.5–2 mm. long. In *M. himalayense* the trichomes on the stems, branches, and leaves are dense, subappressed, and of different lengths, the flowers always sessile, the fruits subsessile or short pedicellate, the thick, stout pedicels never exceeding 2 mm. in length, the bluish-white to pink corolla and the style 0.5–1 mm. long. The specimens cited above are annual, not perennial.

4. **M. thomsonii** (C. B. Clarke) Kazmi, comb. nov.

Paracaryum thomsonii C. B. Clarke in Hook. f. Fl. Brit. India **4**: 161. 1883; Brand, Pflanzenr. IV. **252** (Heft 78): 48. 1921.

TYPE: Alpine western Tibet: Nubra, Baltal, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (K–as *Echinospermum* no. 2).

Robust perennial with roots and lower part of the stems woody, up to 50(–100?) cm. tall. Stems usually many, erect, much branched, branches spreading, stems and branches densely covered with patent, white trichomes 0.5–1 mm. long, arising from minute inconspicuous tuberculate bases. Basal leaves many, forming rosettes, petiolate, (including petioles) 100–140 mm. long, 30–45 mm. broad, ovate to oblong-ovate, coriaceous, gradually or abruptly narrowed into a petiole towards the base, (petiole usually shorter than the lamina) entire, cuspidate, midrib and veins prominent on the lower surface, covered sparsely on the upper surface, densely on the lower surface with short, patent, white trichomes, arising from prominent, white, tuberculate bases, petioles with longer trichomes on the margins towards the base; lower cauline leaves more or less like the basal ones, upper cauline leaves sessile, much shorter and narrower. Inflorescence terminal or axillary short in flower, elongated in fruit, spreading; peduncles usually with one or two bracts. Pedicels lacking to 0.5 mm. long in flower, (1)2–3(–5) mm. long in fruit, stout, horizontal to sometimes reflexed. Calyx divided nearly to the base, lobes ovate, obtuse, hairy externally, glabrous internally 2.5–3 mm. long and 1–1.5 mm. broad, not much elongated in fruit. Corolla white, in dried specimens 2.5–3.5 mm. long, campanulate, limb equalling or little shorter than the corolla tube.

lobes 1.25 mm. long and broad, sometimes broader; faucal appendages subquadrate, emarginate. Anthers attached to the middle of the corolla tube. Nutlets 5–6 mm. long, 4–5 mm. broad, broadly ovate, winged at the margins, wings 1–1.5 mm. broad, plane at the margins to very slightly recurved, broadly dentate, teeth triangular, bearing glochidia at apex, dorsal middle area vertically appendiculate, appendages glochidiate. Style up to 1 mm. long.

DISTRIBUTION: Kashmir, Tibet.

Kashmir: LADAK: near Kharbu, 3000 m., *R. R. Stewart 21106* (GH); Olding near Indus river, 2800 m., *R. R. Stewart 21032* (GH).

5. **M. tibeticum** (C. B. Clarke) Brand, Repert. Sp. Nov. **14**: 156. 1915; Pflanzenr. IV. **252** (Heft 78): 66. 1921.

Paracaryum tibeticum C. B. Clarke in Hook. f. Fl. Brit. India **4**: 162. 1883.
P. tibeticum var. *schlagintweitii* Brand, Pflanzenr. IV. **252** (Heft 78): 66. 1921, *syn. nov.*

TYPE: Ladakh, 12000–14000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (K-holotype, BM-, GH-isotypes, as *Omphalodes* no. 6).

Annual, erect to ascending herb, to 35 cm. tall. Stems solitary or few, more or less dichotomously branched, branches long, suberect to spreading, covered densely on the lower parts with spreading trichomes to 1 mm. long, arising from minute tuberculate bases and on the upper part with short, antrorsely appressed trichomes to 0.5 mm. long, apparently not arising from tuberculate bases. Basal leaves oblong to oblong-ovate, gradually narrowed towards the base into a short petiole, to 6 cm. long and 5–7 mm. broad, covered on both surfaces with short white trichomes arising from prominent white tuberculate bases; lower cauline leaves oblong-lanceolate with shorter petioles; upper cauline leaves sessile, much shorter and narrower. Inflorescence terminal, lax, elongated in fruit. Pedicels erect, hairy, lacking or to 0.5 mm. long in flower, 2–3 mm. long in fruit, rarely those of the lowermost fruits elongated to 6 mm., reflexed. Calyx divided to the base, lobes in flower erect, 1–1.5 mm. long, spreading or reflexed in fruit, 2.5 mm. long. Corolla light to deep blue, cylindrical-campanulate, ca. 2 mm. long, limb subequal to the corolla tube, lobes roundish, spreading; faucal appendages broader than long. Anthers attached to the middle of corolla tube. Fruit orange-red. Nutlets ovoid, 3–4 mm. long, 2.5–3.5 mm. broad, winged at the margin, wings ca. 1 mm. broad, plane at the margins, distantly minutely dentate, teeth at apex not glochidiate, middle dorsal area tuberculate to vertically appendiculate, appendages glochidiate at their apices. Style 0.5–1 mm. long.

DISTRIBUTION: West Pakistan, Kashmir, west Tibet.

West Pakistan: GILGIT AGENCY: Baltistan, Indus River Valley, 10 miles east of Skardu, 2600 m., *Webster & Nasir 5857* (GH); Skardu, 2600 m., *R. R.*

Stewart 20403 (GH); from Hushe to Sospor, *Schlagintweit 6006* (G-type of var. *schlagintweitii*).

Kashmir: LADAKH: Mulbekh, Rabila, *Koelz 6155, 6129a* (MICH); Marsho, *Koelz 6385* (MICH); Lamayuru, 3800 m., *Osmaston 143* (K); Ladakh, *Thomson s.n.* (GH, BM, K-as *Omphalodes* no. 6).

Brand (l. c., 1921) recognized the plants with much longer pedicels (*Schlagintweit 1006*) as var. *schlagintweitii*. The length of fruiting pedicels is quite variable and the specimen cited above represents the variation with the longest pedicel. This has also been mentioned by Clarke (l. c., 1883) in the original description of *P. tibeticum* as "lower pedicels in fruit occasionally ¼ in."

6. **M. bungei** (Boiss.) Rech. f. & H. Riedl in Køie & Rechinger, Biol. Skr. **13**(4): 209. 1963; Riedl in Rechinger, Fl. Iranica **48**: 121. 1967.

Echinospermum bungei Boiss. Fl. Orient. **4**: 252. 1875.
Paracaryum bornmülleri Brand, Repert. Sp. Nov. **14**: 149. 1915.
Paracaryum bungei (Boiss.) Brand, Pflanzenr. IV. **252** (Heft 78): 47. 1921; M. Pop. in Fl. URSS **19**: 605. 1953.

TYPE: *Persia borealis*, prope Shahrud (28 Maio 1868), *Bunge s.n.* (G-holotype, GH-isotype).

ICON.: Riedl, l. c. *fig. 167, 168.* 1963, under *M. tibeticum*; M. Pop. l. c. *t. 29. fig. 3.* 1953, under *Paracaryum bungei.*

Annual, erect, ascending or sometimes prostrate herb. Stems solitary to few, to 25 cm. long, usually branched near the base, branches long; stem and branches covered on the lower part with spreading, on the upper part with antrorsely appressed to subappressed, white trichomes to 1 mm. long, arising from prominent tuberculate bases. Basal leaves 1–2, narrowly oblong to narrowly lanceolate, obtuse, short petiolate, 10–15 mm. long and 1.5–2 mm. broad; lower cauline leaves lanceolate to subspathulate, subsessile or very short petiolate, obtuse to acutish at apex, narrowed towards the base, 10–13(–18) mm. long, 2–3(–6) mm. broad, covered on both surfaces with short, thin, white trichomes arising from tuberculate bases; upper cauline leaves shorter and narrower. Inflorescence lax, much elongated in fruit. Pedicels hairy, lacking in flower, elongated to 6 mm. in fruit. Calyx divided to the base, lobes lanceolate, hairy, ca. 1.5 mm. long in flower, 2–3 mm. long in fruit. Corolla blue, to 2 mm. long, tubular-campanulate, tube equalling the sepals, limb short, lobes subpatent; faucal appendages broader than long, emarginate. Nutlets ovoid, up to 4 mm. long, up to 3 mm. broad, winged at the margins, wings narrow, slightly curved at the edges, dentate, teeth glochidiate at the apex, dorsal middle area vertically appendiculate, appendages glochidiate at apex. Style to 0.5 mm. long.

DISTRIBUTION: Iran, Afghanistan, West Pakistan, Pamir Alaj, Kizil Kum.

West Pakistan: KALAT DIST.: Basima, between Panjgur and Surab, 1350 m. *Kazmi s.n.* (PES); *Rechinger 28281* (W); between Surab and Kalat, 10 kms. from Kalat, *Lamond 681* (E); Shalku, *Jafri & Akbar 2936* (E). MAKRAN DIST.: between Panjgur and Surab, near Nag, 1300 m., *Kazmi 1258* (GH, PES); *Rechinger 28260* (W); Panjgur, Irrigation Scheme, sandy river bed below Dams, 1000 m., *Kazmi 1208b* (PES); *Lamond 604* (E). QUETTA DIST.: between Padag and Nushki, 1200 m., *Lamond 169* (E); *Rechinger 27335* (W). ZHOB DIST.: Fort Sandeman to Wana, 26 km. from Fort Sandeman, between Zhob and Sambaza, 1500 m., *Kazmi 1920a* (PES); *Lamond 1755* (E); *Rechinger 29844a* (W). Reported from: Chagai, 60 km. E. Dalbundin, ad radices M. Rus Kuh, *Rechinger 27296* (W).

The characters, which differentiate *Mattiastrum bungei* from its very closely related species *M. tibeticum*, are the marginal wings of the nutlets curved along the side in *M. bungei*, those of *M. tibeticum* being flat. The margins of the wings in both species are dentate, but the teeth are blunt and do not bear glochidia at the apex in *M. tibeticum*, whereas in *M. bungei* the teeth are slightly produced and do bear glochidia at the apex. The plants of *M. tibeticum* are stouter and erect as compared to the weak stems, and branches of *M. bungei*. The former usually have many basal leaves, the latter have only one or two.

Brand (l. c. 1921) and Riedl (l. c. 1963 & 1967) do not mention the length of the pedicels of *M. bungei*. In the isotype (Shahrud, *Bunge* (GH)) the pedicels of the lower fruits are as long as 15 mm., a condition I did not find in the specimens cited above, only a few of them having pedicels to 6 mm. in length.

23. **Solenanthus** Ledeb. Icon. Pl. Fl. Rossica *t. 26*. 1829; Fl. Alt. 1: 193. 1829.

TYPE SPECIES: *Solenanthus circinnatus* Ledeb.

Perennial or biennial, villous or tomentose herbs. Leaves alternate. Inflorescence terminal or axillary, short thyrsoid, later usually elongated into loose panicles, ebracteate. Flowers pedicellate, pedicels short, later elongated. Calyx divided to the base, lobes hairy, scarcely enlarged in fruit. Corolla cylindrical to funnelform; faucal appendages present. Stamens much exserted from the corolla; anthers subglobose to ovoid. Nutlets ovoid to subglobose, appendiculate at the margins, on the dorsal face or all around, appendages glochidiate, coherent to free from the style.

Species 10 to 14, distributed in southern Europe, central and southwest Asia.

KEY TO THE SPECIES

a. Basal leaves truncate to cordate at the base, abruptly narrowed into the petioles; cauline leaves semiamplexicaul; anthers ca. 0.5 mm. long. . . . . 1. *S. circinnatus*.

a. Basal leaves neither truncate nor cordate at the base, gradually narrowed into the petioles; cauline leaves sessile; anthers ca. 1 mm. long. . . 2. *S. stamineus*.

1. **S. circinnatus** Ledeb. Fl. Alt. **1**: 194. 1829, Icon. Pl. Fl. Rossica *t. 26.* 1829; DC. Prodr. **10**: 164. 1846; Boiss. Fl. Orient. **4**: 270. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 160. 1883; Aitch. Bot. Afgh. Delim. Comm. 88. 1888; Brand, Pflanzenr. IV. **252** (Heft 78): 157. 1921; M. Pop. in Fl. URSS **19**: 642. 1953; Riedl in Rechinger, Fl. Iranica **48**: 131. 1967.

Solenanthus amplifolius Boiss. Diagn. Pl. Orient. **11**: 126. 1849; Fl. Orient. **4**: 270. 1879.

S. rumicifolius Boiss. Dec. Pl. Nov. Orient. **2**: 9. 1875.

S. stamineus (Desf.) Wettst. var. *cuneatifolius* Bornm. Beih. Bot. Centralbl. **20b**: 193. 1906.

TYPE: In regionibus orientalibus ad fl. Irtysch. *C. A. Meyer s.n.* (LE).

ICON.: Ledeb. Icon. Pl. Fl. Rossica *t. 26.* 1829; M. Pop. l. c. *t. 37.* 1953; Riedl, l. c. *t. 46. fig. 1.* 1967.

Perennial, erect herb, 30–120 cm. tall. Stem simple, striate, fistulous, covered loosely to densely with soft, crisped white trichomes. Basal leaves, petiolate, (including petioles) 10–60 cm. long, (2–)5–10(–14) cm. broad, elliptic-oblong to oblong-lanceolate, obtuse to acutish, at the base usually cordate, sometimes truncate, loosely or densely pubescent on both surfaces, on the lower surface sometimes with some scattered trichomes arising from minute tuberculate bases, upper surfaces rarely glabrous; cauline leaves much reduced in size, usually sessile, cordate at the base, semi-amplexicaul, loosely or densely pubescent on both surfaces. Inflorescence congested, capitate in young plants, later thyrsoid or rarely loose paniculate, ebracteate. Pedicels short. Calyx densely pubescent, divided to the base, lobes oblong-ovate to oblong-lanceolate, obtuse to subacute, 3–5 mm. long in flower, not much enlarged in fruit. Corolla blue, 4.5–6 mm. long, cylindric-infundibuliform, lobes triangular, subacute, erect, ca. 1 mm. long; faucal appendages oblong, developed below the middle of the corolla tube. Anthers ovate, 0.5 mm. long; filaments at the base not at all to conspicuously dilated, ca. 5 mm. long, much exserted from the corolla. Nutlets ovoid, obtuse, 6–7 mm. long, dorsally irregularly appendiculate, appendages glochidiate.

DISTRIBUTION: Iraq, Iran, Afghanistan, West Pakistan, Kashmir; Caucasus, Turkestan, Pamir Alaj, Siberia, Tien Shan, Dsungaro-Tarbagatai.

West Pakistan: CHITRAL STATE: Rumbur, *Bowes Lyon 663* (BM, E); Ziarat, Lowari Pass, 2600 m., *Stainton 2339* (BM); Agram, Arkari Gol, west Tirichmir, 3150 m., *Stainton 2634* (BM, E); Shigar Arirat, 2850 m., *Bowes Lyon 758* (BM). Reported from: Chitral, Barum Gol, Shokor Shal, 3500 m., *Wendelbo s.n.*

Kashmir: LADAK: Dras, 3500 m., *Ludlow & Sherriff 8319* (GH); Zanskar, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH). Reported from: Pangee, *Watt s.n.*; Ladakh in Chilungtal, *Meebold 4242.*

2. **S. stamineus** (Desf.) Wettst. Denkschr. Akad. Wiss. Wien **50**(2): 88. 1885; Brand, Pflanzenr. IV. **252** (Heft 78): 155. 1921; M. Pop.

in Fl. URSS **19**: 652. 1953; Riedl in Rechinger, Fl. Iranica **48**: 133. 1967.

Cynoglossum stamineum Desf. Ann. Mus. Hist. Nat. Paris **10**: 431. 1807.
Mattia staminea Roem. & Schult. Syst. Veg. **4**: 82 & 764. 1819.
Moltkia libanotica Zucc. Abh. Acad. Wiss. München **3**: 246. 1837–1843.
Solenanthus tournefortii DC. Prodr. **10**: 164. 1846.
Solenanthus conglobatus DC. *Ibid.* 166.
Solenanthus strictissimus Brand, Repert. Sp. Nov. **13**: 546. 1915; Pflanzenr. IV. **252** (Heft 78): 156. 1921; Riedl in Rechinger, Fl. Iranica **48**: 133. 1967, *syn. nov.*

TYPE: Cappadocia, *Tournefort s.n.* (P).

ICON.: Brand, l. c. *fig. 21.* 1921.

Perennial, erect herb, to 70 cm. tall. Stem simple, striate, fistulous, covered loosely or densely with soft, patent or retrorsely subappressed white trichomes. Basal leaves petiolate, (including petioles) to 45 cm. long and 3.5(–6) cm. broad, lanceolate to oblong-lanceolate, acute to subacute, at the base narrowed into a long petiole, 3–5-nerved, nerves prominent below and covered on the upper surface loosely, on the lower surface densely with short, crisped, white trichomes, the nerves with dense, subappressed trichomes; middle cauline leaves sessile, shorter and narrower; upper cauline leaves shorter and broader. Inflorescence terminal or in the axils of the upper leaves, congested in short, cylindrical thyrses when young, later elongated, ebracteate. Pedicels lacking in flower, up to 2 mm. long in fruit. Calyx divided to the base, lobes 2–4(–5) mm. long, ca. 1 mm. broad, oblong-lanceolate, obtuse, erect, pubescent. Corolla dark red to rarely yellowish, 5–6(–7) mm. long, cylindrical, lobes 0.5 mm. long, 1 mm. broad at the base, triangular to broad-ovate, erect; faucal appendages subquadrate, emarginate, developed at the middle of the corolla tube. Filaments up to 5 mm. long, slightly dilated at the base, inserted at the middle of the corolla tube; anthers 1 mm. long, ovate, much exserted from the corolla. Nutlets ca. 10 mm. long, ovoid, at the margins densely, and at the dorsal middle area sparsely appendiculate, appendages glochidiate at apex.

DISTRIBUTION: Greece, Turkey, Syria, Lebanon, Iraq, Iran, Caucasus, Afghanistan, West Pakistan, Pamir Alaj.

West Pakistan: CHITRAL STATE: Serer, 3300 m., *Bowes Lyon 791* (BM, E); Agram, Arkari Gol, west of Tirichmir, 3330 m., *Stainton 2627* (BM). HAZARA DIST.: Kagan Valley, Kamalban forests, *Kazmi s.n.* (PES); Kagan Valley, Narang, 3. 6. 1927, *Champion s.n.* (GH). GILGIT AGENCY: Plants of Gilgit Expedition (*Solenanthus* = *5980* Griffith, Kew Distrib.), *Giles s.n.* (E-type of *S. strictissimus*).

Brand (l. c. 1915, 1921) distinguishes *Solenanthus strictissimus* from *S. stamineus* by its linear, basal leaves to 10 cm. long and by its corolla and calyx lobes 1 mm. shorter. The primary basal leaves in *S. stamineus* are also linear and short, they dry and fall away as soon as the secondary

basal leaves appear. The secondary basal leaves, which are found on most collections are much longer and broader than the primary leaves. *Solenanthus strictissimus* is based on the only collection of Giles from Gilgit Agency and no other collection of this species has been made since. It appears that one of the early leaves, which is shorter and narrower, left attached to the type collection, led Brand to recognize it as a distinct species. As there are no differences in the form and indument of the cauline leaves and the structure and measurements of the floral parts, I consider *S. strictissimus* to be a synonym of *S. stamineus*.

[*To be continued*]

THE GENUS NEILLIA (ROSACEAE) IN MAINLAND ASIA AND IN CULTIVATION

J. Cullen

My attention was drawn to the genus *Neillia* by an attempt to identify three specimens growing at the University of Liverpool Botanic Gardens, Ness, Neston, Cheshire. The standard works for the identification of garden shrubs all seemed unsatisfactory as far as this genus was concerned. This led me to borrow herbarium material for comparison and study, and to write to various gardens, asking for specimens of all their Neillias for inclusion in a taxonomic survey of the genus.

Comparison of the herbarium material with the relevant taxonomic literature (particularly Vidal's revision of the genus, in Adansonia II. 3: 1963) revealed that many specimens had never been named, and led me to a reappraisal of the species, as represented by both herbarium and garden material.

The genus *Neillia* is the type genus of the small tribe Neillieae of the subfamily Spiraeoideae of the Rosaceae. Its closest allies are *Stephanandra* and *Physocarpus*, both of which contain species in cultivation. The distinctions between these genera are not great, and errors appear in most of the accounts. The most satisfactory key to their identification is that provided by Vidal (*op. cit.*), on which the following one is based.

1. Carpels 5–3(–1); follicles dehiscent along both sutures. .... *Physocarpus.*
1. Carpels 1–2(–5); follicles dehiscent along the ventral suture only.
   2. Style terminal; follicle 2–10-seeded; testa smooth and shining. ..... *Neillia.*
   2. Style at last lateral; follicle 1–2-seeded; testa crustaceous. ..... *Stephanandra.*

Defined as in this key, the genus consists of shrubs (one species suffrutescent) of arching habit, with lobed, serrate leaves, and racemes or panicles of white or pink flowers. A flowering bush has a strong superficial resemblance to a *Ribes*, and, in gardens, Neillias tend to be grown in mixed shrubberies and semiwild areas. Vidal, treating the whole area of the genus, recognizes 13 species; I have seen material only from the mainland of Asia (the genus occurs also in Java and Sumatra), and in this area I recognize ten species, which correspond to twelve of those maintained by Vidal.

Most of the characters used in the taxonomic treatment of the genus are straightforward, and have been described by Vidal. In addition, however, I have found the mode of branching to be very useful in dividing the genus into two parts, and as the branching is unusual, and to my knowledge has not been described before, I give some explanatory notes here.

MODE OF BRANCHING

The following observations were made on mature bushes of *Neillia thibetica* and *N. sinensis* var. *ribesioides* growing at Ness, supplemented by studies of herbarium material.

Mature bushes of these two species consist of a large number of old, woody, brown-barked stems, leafless at the base, arising from ground level. These old stems, which may reach 15 feet (45 dm.) or more, are usually markedly zigzag, especially in the upper part, and their apices are apparently dead, as each ends in a short, dry extension without obvious buds. Alternate leaf scars are present on these stems, and in their axils are multiple, superposed buds, of which generally three or four are visible, the uppermost being some distance (often about 1 cm.) above the actual leaf scar.

The plants are deciduous, and in winter completely leafless. As spring advances buds borne near the apices of the old shoots begin to develop; in all cases the uppermost bud of each axil develops first. These growths develop into the short shoots bearing the inflorescences, and quite early in the spring the young flower buds may be seen terminating the short, leafy shoots. By about the end of May these shoots reach their maximum extension and the flowers open. Each flowering shoot is markedly perulate at the base, with hard, persistent bud-scales; bears from three to seven leaves, and is terminated by the raceme. The leaves on these shoots of limited growth have only *one* bud in each axil.

As the flowers mature, and the fruits develop, one of the lower buds from the axil which produced the flowering shoot begins to develop, as do buds in the lower parts of the woody stems. These buds develop into vegetative shoots of unlimited growth, which extend rapidly, and again, have multiple, superposed buds in their leaf axils. After the release of the seeds, the whole of the flowering shoot is often shed, leaving the vegetative shoot which developed from the same axil, and those from below, to persist through the winter.

In *Neillia sinensis* var. *ribesioides* the leaves on the flowering shoots are smaller and more deeply lobed than those on the vegetative shoots, whereas in *N. thibetica* there is little difference between leaves from the two types of shoot.

Thus, in both these species there is a shoot dimorphism, with the earlier flowering shoots, which are of limited growth, being formed from the uppermost buds of each group and terminating in an inflorescence, with each leaf having one bud in its axil. The later vegetative shoots, are formed from the lower buds of a group, are of unlimited growth, with each leaf having multiple, superposed buds in its axil.

As far as can be judged from herbarium material (which is usually collected in the flowering stage) a similar situation is found in all the other species of the genus with the exception of *Neillia thyrsiflora*, *N. serratisepala*, and probably *N. fallax*. In these species the dimorphism between vegetative and flowering shoots is not so marked, and the leaves

on the long flowering shoots bear multiple buds in their axils. The flowering shoots are not perulate at the base, and in general, are more leafy. The exact behavior of these species is in doubt, as I have not seen living plants of any of them, but they clearly form a distinct group, easily separable from the other species.

Multiple superposed buds occur in the one species of *Stephanandra* I have seen (*S. tanakae* Franch.) but are absent in at least two of the species of *Physocarpus* (*P. opulifolius* (L.) Maxim. and *P. amurensis* Maxim.).

A NOTE ON TERMINOLOGY

The flowers of *Neillia* are of the type generally known as perigynous, i.e., with sepals, petals, and stamens borne on the top of a tubular structure. The nature of this structure has been much debated, and various names have been given to it. For instance, Rehder (Man. Cult. Trees & Shrubs, 1927) refers to it as "calyx tube," whereas Vidal (*op. cit.*) calls it "hypanthium." Both of these terms have morphological implications which are not certainly valid in the case of *Neillia*, and I have therefore used the neutral term "floral tube."

GROUPING OF THE SPECIES

In a genus of this size there seems relatively little point in recognizing subgenera or sections. The ten species treated here, do however, fall into four more or less clearly defined groups:

1) *Neillia thyrsiflora* group. This consists of certainly two and possibly three species. *N. thyrsiflora* and *N. serratisepala* are closely related, and clearly belong together. The Javanese and Sumatran *N. fallax* Blume, which I have not seen, probably also belongs here, as it has been frequently confused with *N. thyrsiflora*, which also occurs on both Java and Sumatra. The group is characterized by its branching (see above), its strigose floral tube, and its white flowers.

2) *Neillia affinis* group. Again consisting of two species, the polymorphic *N. affinis* and the closely allied and vicariant *N. rubiflora*. The usually pink flowers have a globose-campanulate floral tube as broad as, or broader than long. The carpels contain three or more ovules.

3) *Neillia lobata* group. This is a rather variable group containing three species, *N. lobata*, *N. uekii*, and *N. gracilis*. The one common character is the occurrence of only two ovules per carpel. The flowers are pink or whitish, and the floral tube is short and cylindric-campanulate.

4) *Neillia sinensis* group. Another group of three species, including the polymorphic *N. sinensis*, *N. thibetica*, and *N. sparsiflora*. It is characterized by a long cylindrical floral tube, carpels with three or more ovules, and usually pink flowers. This group is taxonomically the most complex in the genus (except for *N. sparsiflora*, which is a perfectly distinct species) and the present account of it differs considerably from that of Vidal.

As originally described, *Neillia sinensis* and *N. thibetica* differed in a number of characters as shown below:

	N. sinensis	*N. thibetica*
Floral tube	long, glabrous outside	shorter, pubescent outside
Pedicels	long	short
Inflorescence	lax, few-flowered	dense, usually many-flowered

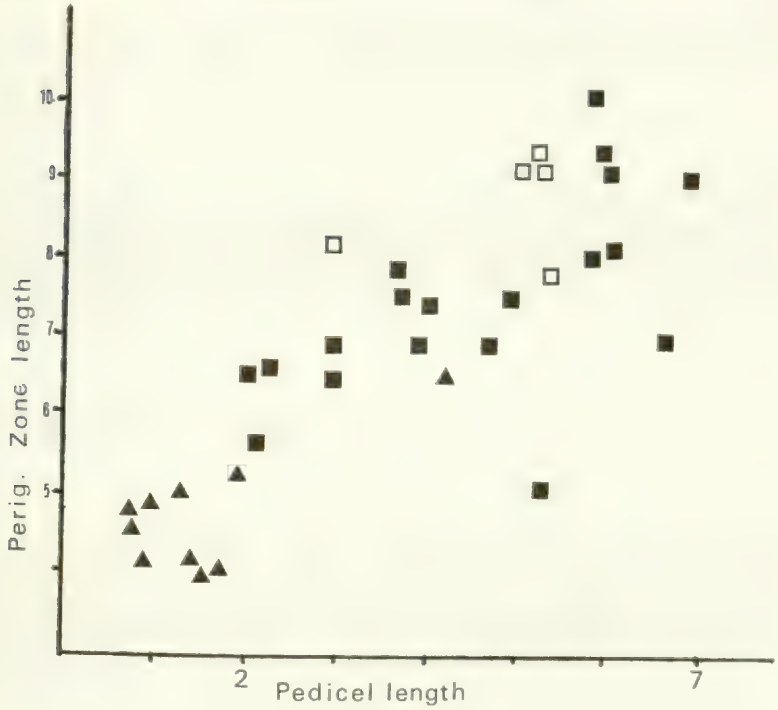
As more and more specimens were collected, these distinctions became blurred, and the identification of individual specimens became more difficult. In attempting to deal with this situation more taxa were described, either at the specific or varietal level. These included *N. longiracemosa* Hemsl. (1892), *N. glandulocalyx* Lévl. (1914–15), *N. ribesioides* Rehder (1913), *N. sinensis* var. *caudata* Rehder (1913), *N. villosa* W. W. Sm. (1917), and *N. hypomalaca* Rehder (1932) (*N. sinensis* var. *hypomalaca* (Rehd.) Hand.-Mazz., 1933).

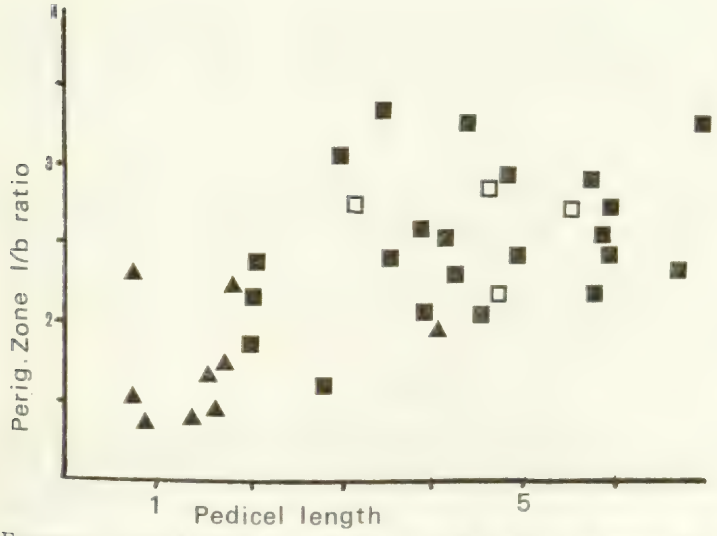
No attempt was made to evaluate these taxa until Vidal's paper of 1963 (Handel-Mazzetti's treatment in *Symbolae Sinicae* being largely compilation). Vidal recognizes the following taxa: *N. glandulocalyx* Lévl., *N. sinensis* Oliv. (with vars. *sinensis*, *ribesioides* (Rehd.) Vidal, and *hypomalaca* (Rehd.) Hand.-Mazz.), *N. villosa* W. W. Sm., and *N. thibetica* Bur. & Franch. (*N. longiracemosa* Hemsl.) with vars. *thibetica*, *duclouxii* Vidal, and *caudata* (Rehd.) Vidal. In discriminating between the four species recognized, Vidal lays great stress on the number of ovules per carpel: 4 or 5 in *Neillia glandulocalyx* and *N. sinensis*, 5 to 8 in *N. thibetica*, and 5 or 6 in *N. villosa*. This interpretation considerably alters the original distinctions, both *N. sinensis* and *thibetica* here including forms with hairy or glabrous floral tubes. Other characters used by Vidal in discriminating between the taxa include indumentum, leaf-shape, stipule toothing, pedicel length and indumentum, and petiole length.

I found many specimens difficult to identify by this classification and therefore undertook an analysis of all the complete specimens available to me, a total of about 40 (a complete specimen being one with both leaves and well-developed flowers; changes after fertilization render fruiting specimens unsuitable). Each specimen was scored for the following characters: indumentum, length, and length/breadth ratio of the floral tube; indumentum and length of pedicel; density of indumentum on the lower surface of the leaf; number of flowers per inflorescence; number of ovules per carpel. FIGURES 1 to 4 show some of the variation in pictorialized scatter-diagram form.

This analysis shows that in this whole group of specimens there is no pair of completely correlated characters by which one may divide the group. There is, however, a close approach to this with a number of characters, enabling a good separation into two units to be made:

a) Floral tube glabrous or with a few patent trichomes, (5–)6 mm. or more long; pedicels (2–)3–7 mm. long; 10–17(–23) flowers per inflorescence.





FIGURES 1 (above) and 2 (below). Variation in the *Neillia sinensis*/*N. thibetica* group. ▲ floral tube pubescent; □ floral tube with few patent trichomes; ■ floral tube glabrous. (All measurements in mm.) On graphs for "Perig. Zone" read "Floral tube".

b) Floral tube finely pubescent, up to 6 mm. long; pedicels 0.6–2(–3) mm. long; (19–)24–60 flowers per inflorescence.

Two facts are immediately apparent: 1) ovule number is in no way correlated with any of the other characters (cf. FIGURE 4); 2) the two taxa defined above correspond closely with the original conceptions of *Neillia sinensis* and *N. thibetica*. These correlations break down in the case of only a few specimens, indicating perhaps, occasional hybridization.

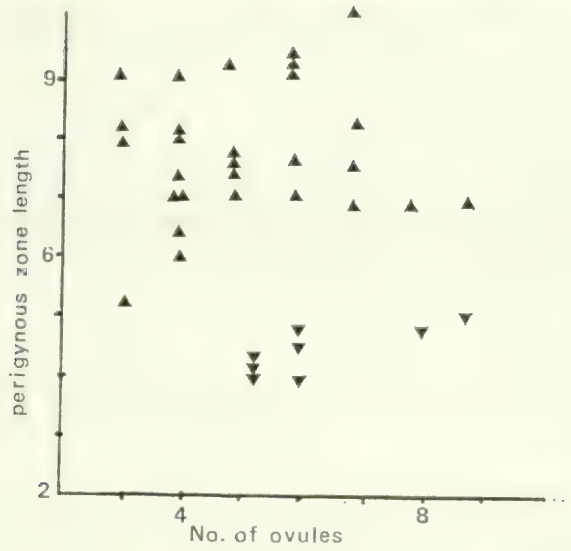
As a result of these studies, I recognize only two species in this group, *Neillia sinensis* and *N. thibetica*. *Neillia thibetica* appears as a very uniform taxon, showing little variation. Of the varieties recognized by Vidal, var. *caudata* goes with *N. sinensis* (as originally described by Rehder), having long, glabrous, long-pedicelled flowers in few-flowered inflorescences. Varietas *duclouxii* is a problem. Vidal describes it as having a glabrous floral tube (". . . *calycis tubo glabro*"), which would indicate its relationship to *N. sinensis*: but the one specimen I have seen cited by him as var. *duclouxii* (*Wang 23084*) has a finely pubescent floral tube and differs in no essential way from typical *N. thibetica*.

As opposed to *Neillia thibetica*, *N. sinensis* is polymorphic, varying in flower size, leaf shape, and indumentum of all parts. The specimens can easily be separated into two groups: the sparsely hairy or glabrous (referring to leaves, pedicels, and floral tubes) and the densely hairy. Such a division is somewhat subjective as there is no clear discontinuity in the variation, but individual specimens are usually easily assignable to one or the other group. What is remarkable is that variations in other characters in the hairy and sparsely hairy lots parallel each other in a most striking way. Thus, in each there is a subgroup with ovate, more or less cordate, toothed stipules and usually little-lobed, long-attenuate or caudate leaves; a subgroup with small flowers, and smallish, lobed leaves; and a subgroup (the remainder) without any of these distinguishing characteristics. Because the main character dividing these six subgroups is not amenable to precise analysis, and the other characters show some overlap and intergradation, I have recognized six varieties in *N. sinensis*, grouped in the following way: 1) glabrous or sparsely hairy: vars. *sinensis*, *caudata* Rehd., and *ribesioides* (Rehd.) Vidal; and 2) densely hairy: vars. *hypomalaca* (Rehd.) Hand.-Mazz., *villosa* (W. W. Sm.) Cullen, and *rosea* Cullen. Additional details are given in the taxonomic revision.

TAXONOMY

Neillia D. Don, Prod. Fl. Nepal. 228. 1825.

Suffrutescent herb or, more usually, arching shrubs up to 6 m., usually hairy in at least some part. Shoots usually dimorphic. Leaves alternate, entire or lobed, irregularly serrate, stipulate, stipules deciduous or persistent, entire or toothed. Axillary buds multiple and superposed, at least on vegetative shoots. Inflorescences racemose or paniculate. Flowers bracteate, pedicellate, with a cylindric to campanulate floral tube (hypan-



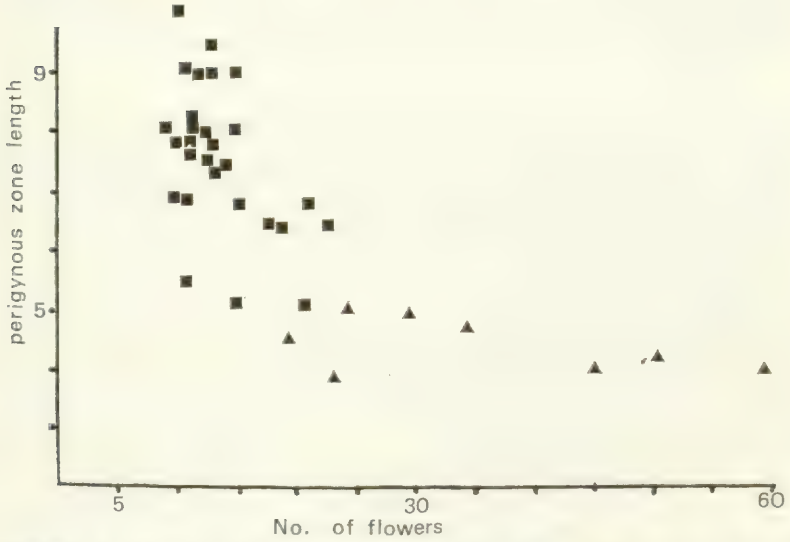


FIGURE 3 (above). Variation in the *Neillia sinensis/N. thibetica* group. ▼ floral tube pubescent; ▲ floral tube glabrous.

FIGURE 4 (below). Variation in the *N. sinensis/N. thibetica* group. ▲ floral tube pubescent; ■ floral tube glabrous. (All measurements in mm.) On graphs for "perigynous zone" read "floral tube".

thium or calyx tube of authors), glabrous, sparsely patent-pilose, pubescent or strigose outside, pilose within below the insertion of the stamens. Nectar secreted near the base of the floral tube. Sepals 5, pubescent on

the inner surface. Petals 5, white or pink, very shortly clawed, erose-ciliate on the margins, sometimes pubescent on the inner surface. Stamens (10–)15–30, in two or three series, inflexed in bud. Carpels 1(–2–5), free when more than one, ovules 2–10 per carpel. Fruit a follicle or group of follicles opening along the ventral suture, enclosed in the persistent, accrescent floral tube, which often develops an additional indumentum of long, spreading, capitate-glandular bristles after fertilization. Seeds several, shining, pale brown. LECTOTYPE SPECIES: *Neillia thyrsiflora* D. Don.

1. Leaves on the flowering shoots with multiple, superposed buds in their axils; floral tube strigose; petals white.
   2. Ovary velutinous; ovules 3–4. ..... 2. *N. serratisepala.*
   2. Ovary glabrous or hairy at the apex only, rarely totally pubescent; ovules 8–10. ..... 1. *N. thyrsiflora.*
1. Leaves on the flowering shoots with one bud in their axils; floral tube glabrous or variously hairy but not strigose; petals usually pink.
   3. Floral tube globular-campanulate at anthesis, as broad as or broader than long.
      4. Carpels 1–5, pubescent all over the surface, narrowing abruptly into the style. ..... 3. *N. affinis.*
      4. Carpels 1, pilose only at apex, tapering gradually into the style. ..... 4. *N. rubiflora.*
   3. Floral tube cylindric or cylindric-campanulate, always longer than broad.
      5. Short shoots with an indumentum of capitate-glandular hairs. ..... 8. *N. sparsiflora.*
      5. Short shoots without capitate-glandular hairs.
         6. Suffrutescent herb, up to 30 cm. high, with creeping, rhizomatous shoots (ovules 2). ..... 5. *N. gracilis.*
         6. Shrubs with woody aërial branches, without creeping, rhizomatous shoots, much exceeding 30 cm.
            7. Branches and inflorescence axis with an indumentum of sparse, finally deciduous, tuberculate-based, stellate hairs (ovules 2). ..... 6. *N. uekii.*
            7. Branches and inflorescence axis glabrous or with an indumentum of simple, etuberculate hairs.
               8. Bark of old shoots puberulent; leaves lobed to 2/3 of the width of lamina; ovules 2. ..... 7. *N. lobata.*
               8. Bark of old shoots glabrous; leaves less deeply lobed; ovules 3 or more.
                  9. Floral tube glabrous or with sparse patent hairs near the base; flowers 10–17(–23) per inflorescence. ..... 9. *N. sinensis.*
                  9. Floral tube finely pubescent all over the surface; flowers (19–)24–60 per inflorescence. ..... 10. *N. thibetica.*

1. **Neillia thyrsiflora** D. Don, Prodr. Fl. Nepal. 228. 1825; Vidal, Adansonia II. 3: 152. *pl. 1, figures 3–6.* 1963. FIGURE 5: 17, 18.

N. virgata Wall., *nomen nudum.*

Ovary glabrous or sparsely pilose at the apex and along the sutures; panicles usually much branched. ..... var. *thyrsiflora.*

Ovary pubescent over most of the surface; panicle usually little branched. . . . . var. *tunkinensis*.

Var. thyrsiflora

India. Khasia hills, *Watt* (E); ibid., *Kurz* (E); ibid., 1500–2000 m., *Hooker & Thomson* (E); ibid., Cherrapunji, 1600 m., 1878, *Gallatly 214* (A); ibid., Mulki, 1750 m., 12 June 1923, *Ruse* (A); Gitjhora, W. of Jaldahar, 12 Feb. 1900, *Cave 56* (E); Assam, *Simons* (E); W. Bengal, E. Himalayas, Ghoom, 2500 m., 4 July 1919, *Cave* (E); ibid., Labdah, 1500 m., 24 Jan. 1923, *Cave* (E); ibid., 1000 m., 10 Oct. 1912, *Cave* (E); ibid., 1500 m., 4 Aug. 1922, *Cave* (E); E. Himalaya, Singmari, 8 May 1940, *Biswas* (A); Kataphar, 2300 m., 28 Dec. 1937, *Anon.* (A, NA); Manipur, Sereepharai, 2600 m., 16 Jan. 1882, *Watt* (E); ibid., Chamoo, 1500 m., 14 Jan. 1882, *Watt* (E); Darjeeling, *Lace 2347* (E); ibid., 1905, *Drummond 21043* (E); ibid., *Cowan* (E); ibid., Lahagach, 5 Aug. 1923, *Cowan* (E); ibid., Sinchal lake, ca. 2800 m., 15 Nov. 1944, *Relzada 19034* (A); Kurseong, 1903, *Brühl* (E).

Sikkim. Regio temp., 2000–2600 m., *Hooker* (A, E); Gassing to Ratong river, 2 Oct. 1882, *Anderson 505* (E); Sureil, 1800 m., 29 Aug. 1912, *Cave* (A); Mungpoo, 1300 m., 28 July 1909, *Cooper 556* (A). **Bhutan.** Chukha Tunpu, 1500 m., 4 July 1914, *Cooper 1229* (E); Tongsa, 2600 m., 11 Sept. 1914, *Cooper 2069* (E); Tilageng, Punabha, 2100 m., 18 Aug. 1914, *Cooper 2814* (E); sine loc., *Griffith* (E). **Nepal.** Sine loc., *E.J.C.* (E); Gurke Bandhara to Charikot, 2000 m.,10 Oct. 1960, *Banerji 1210* (A). **Burma.** Laktang, 1500 m., 21 June 1919, *Kingdon-Ward 3241* (E). **Tibet.** Raiotdong to Santok, 800–2000 m., 27 June 1903, *Younghusband* (A).

China. YUNNAN: Szemao forest, 1500 m., *Henry 12275* (A, E); S. of Red river, *Henry 13653* (A, E); sine loc., 1939–40, *Wang & Liu 81820* (A, E); Kiukiang valley (Taron), Monting, 1350 m., 10 Sept. 1939, *Yü 20199* (A, E); ibid., Chiengen, 1650 m., *Yü 19409* (E); above Kan San Chai, W. of the Mekong, en route from Pingpo to Yungchang and Tengyueh, Salween watershed, Oct. 1922, *Rock 7056* (A); Ping Pien Hsien, 1300 m., 7 July 1934, *Tsai 60717* (A); ibid., 1400 m., 15 June 1934, *Tsai 60207* (A); ibid., 7 June 1934, *Tsai 62383* (A); Lu-se, 1750 m., 10 Feb. 1934, *Tsai 56895* (A); ibid., 1750 m., 1 Mar. 1934, *Tsai 56350* (A); Dzung-duei, Cham-pu-lung, 2000 m., Oct. 1935, *Wang 67076* (A) and *66940* (A); Che-tse-lo, 3200 m., *Tsai 58432* (A). KWANGSI: On Tak, 21 Oct. 1935, *Ko 55787* (A).

In addition to the areas mentioned above, Vidal (*op. cit.*, 153) records this taxon from Sumatra.

Var. **tunkinensis** (Vidal) Vidal, Adansonia II. 3: 153. 1963.

N. tunkinensis Vidal, Not. Syst. Paris. **13**(4): 202. 1948.
N. tunkinensis var. *bibracteolata* Vidal, *loc. cit.*

Burma. N. Triangle (Hkinkum), 1300 m., 10 July 1953, *Kingdon-Ward 21135* (A). **China.** YUNNAN: sine loc., *Wang & Liu 83503* (A, E); sine loc., *Forrest 29897* (E); Mengtze, 1800 m., *Henry 9419* (A, E); ibid., S. mts., 1500 m., *Henry 9419A* (E); Mienning, Poshan, 2700 m., 9 Oct. 1938, *Yü 17974* (A, E); Salwin-Kiukiang divide, Newahlung, 2200 m., 8 July 1938, *Yü 19228* (A, E).

Vidal records this taxon from Assam, North Vietnam, Java, and Su-

matra. It appears to be intermediate between *Neillia thyrsiflora* var. *thyrsiflora* and *N. serratisepala*, the only distinct character separating them being the number of ovules (8–10 in both varieties of *N. thyrsiflora*, 3–4 in *N. serratisepala*). I have followed Vidal in treating them as separate species, but there are grounds for considering *N. serratisepala* as merely another variety of *N. thyrsiflora*.

2. **Neillia serratisepala** Li, Jour. Arnold Arb. 25: 300. 1944; Vidal, Adansonia II. 3: 151. 1963.

China. YUNNAN: Shang Pa, 2000 m., 31 Oct. 1934, *Tsai 59158* (A, holotype).

This species is known only from the type collection; for further observations see under *Neillia thyrsiflora*.

3. **Neillia affinis** Hemsl. Jour. Linn. Soc. 29: 304. 1892; Vidal, Adansonia II. 3: 155. 1963.

A polymorphic species, divisible into four varieties:

1. Carpels 3–5, free but contiguous, forming a globose ovary. . . Var. *polygyna*.
1. Carpels 1–2.
   2. Sepals as long as or longer than the floral tube, 4.2–6 mm., much exceeding petals. . . . . Var. *longisepala*.
   2. Sepals shorter than the floral tube, up to 4 mm., not or scarcely exceeding petals.
      3. Raceme elongate, the flowers 10 or more, spaced along the axis. . . . . Var. *affinis*.
      3. Raceme contracted, the 5–10 flowers fascicled at the end of the axis. . . . . Var. *pauciflora*.

Var. **affinis** Vidal, Adansonia II. 3: 155, 156. *pl. 1, fig. 11.* 1963.

FIGURE 5: 15.

China. YUNNAN: Chungkang snow range, 2500 m., 31 July 1938, *Yü 17115* (A, E); Kengma, Chuichayko, 2500 m., 10 Aug. 1938, *Yü 17297* (A, E); Fuchuan Range, W. of Mekong-Salwin divide and W. of Wei Hsi, 3800 m., 4–5′, June 1932, *Rock 22729* (A, E); ibid., July-Sept. 1932, *Rock 23275* (A, E); inter fluvios Landsang-djiang (Mekong) et Lu-djiang (Salween) ca. 28°, in valle a jugo Si-la, ad vicum Tsekuo descendente. 2300–3050 m., 15 June 1916, *Handel-Mazzetti 8884* (A, E); Tengyueh, *Howell 200* (E); sine loc., *Forrest 30023* (E); Yi Liang Hsien, 1400 m., 27 May 1932, *Tsai 52055* (A); Jue-she-hsien, 2500 m., 31 May 1932, *Yü 941* (A); Yong-shan-hsien, 2100 m., 31 May 1932, *Tsai 50949* (A). SZECHUAN: Neighbourhood of Tachienlu, 3000–4500 m., *Pratt 347* (K, syntype); Wa-shan, June and Sept. 1908, *Wilson 916a* (A, E–transition to var. *polygyna*); Opien Hsien, 14 July 1930, *Fang 4694* (A, E); sine loc., Feb. 1890, *Henry 8968* (A, E, isosyntypes); Wu-shan, 2600 m., July 1908, *Wilson 3559* (A); Hsiao-hsiang-ling, 2000 m., 21 May 1922, *Smith 1865* (A); sine loc., 2600 m., July 1904, *Wilson 3560* (A); Nanchuan Hsien, 1928, *Fang 935* (A). SIKANG: Chi-na-tung, Tsa-wa-tung, 3000 m., Aug. 1935, *Wang 65196* (A). **N. Burma.** Moku-ji pass, 3300 m., 28 July 1920, *R. F[arrer] 1757* (E).

Var. **polygyna** Cardot ex Vidal, Adansonia II. 3: 156. *pl. 1, fig. 12.* 1963.

China. YUNNAN: Wei-hsi-hsien, Yeh-chih, 3200 m., mountain slope. Aug. 1935, *Wang 68154* (A); on the Kari pass, lat. 28°N, 4000 m., June 1917, *Forrest 14002* (A, E, WSY).

Also recorded from eastern Tibet by Vidal.

Var. **pauciflora** (Rehd.) Vidal, Adansonia II. 3: 156. *pl. 1, fig. 3.* 1963.

N. pauciflora Rehd. Pl. Wils. 1: 437. 1913.

China. YUNNAN: Mengtze, N. mt., 2300 m., *Henry 10231A* (A, holotype); hills to the E. of Tengyueh, 25°N, 2000 m., May 1912, *Forrest 7854* (A, E); Shweli-Salween divide, 25° 6′ N, 98° 50′ E, 2600 m., *Forrest 29567* (E). SZECHUAN: Mt. Omei, 2300 m., 27 July 1939, *Sun & Chang 1234* (A); ibid., Yen-wang-po, 2400 m., 18 Aug. 1940, *Tu 272* (A).

Var. **longisepala** Cullen, var. nov.

A var. *affinis* sepalis majoribus, 4.2–6 mm. longis, conspicuis differt.

China. YUNNAN: Shweli-Salween divide, 25° 20′ N, 3000 m., shrub of 4–5′, fls. creamy yellow, in scrub and thickets in side valleys, Aug. 1918, *Forrest 17605* (E, holotype; A, WSY, isotypes). SZECHUAN: Ta-hsiang-ling, 2700 m., 28 May 1922, *Smith 2043* (A); Mt. Omi, June 1904, *Wilson 4886* (A, NA). SIKANG: Tsarong, on Doker-la, Mekong-Salwin divide, 28° 20′ N, *Forrest 14342* (A, E, WSY); Doker-la, 3600–4000 m., July 1913, *Kingdon-Ward* (E). **Burma.** Hpimaw village, road to Feng-shiu-ling, 2000–2300 m., forests, 22 May 1914, *Kingdon-Ward 1584* (E).

As is shown by the number of varieties, *Neillia affinis* is a rather polymorphic species. The variations, however, do not seem to be separable geographically. Var. *longisepala* is very distinct in its long conspicuous sepals; it may also differ from the other varieties in having stipules which are more toothed. The latter character is one which can only be determined subjectively, and it is usually of no value in determining specimens in fruit, where the stipules have usually been lost. The inflorescence in *N. affinis* is often a panicle, sometimes richly branched; this has caused some confusion with *N. thyrsiflora*, a perfectly distinct species.

4. **Neillia rubiflora** D. Don, Prodr. Fl. Nepal. 228. 1825; Vidal, Adansonia II. 3: 155. *pl. 1, fig. 9, 10.* 1963. FIGURE 5: 16.

India. E. Himalaya, Sandakpha, 4000 m., 21 July 1913, *Rohmoo Lepcha 766* (E); Darjeeling district, 2300 m., May 1908, *Smith* (A). **E. Pakistan.** Bengal, Chittagong division, nr. Soylu, 3000 m., *Cowan 79* (E). **Sikkim.** Reg. temp., 2600–3000 m., *Hooker* (A, E); ibid., *Schneider* (A); Zemu and Lonakh valleys, Zemu Chu, 3000 m., 6 Sept. 1947, *Cave 97/47* (E); Sureil, 7 Sept. 1921, *Wilson* (A). **Bhutan.** Tobrang (Trashi Yangse Chu), 2300 m., 6 July 1948, *Ludlow, Sherriff & Hicks 20495* (E); Lao (Trashi Yangse Chu), 3000 m., 5 July 1949, *Ludlow, Sherriff & Hicks 20475* (E); Shabjethang, Bumthang Chu, 3000–3200 m., 1 July 1949, *Ludlow, Sherriff & Hicks 19288* (E); Gyasa Dzong, Mo Chu, 3000 m., 12 June 1949, *Ludlow, Sherriff & Hicks 16520* (E). **Nepal.** Sine loc., *E.J.C.* (E).

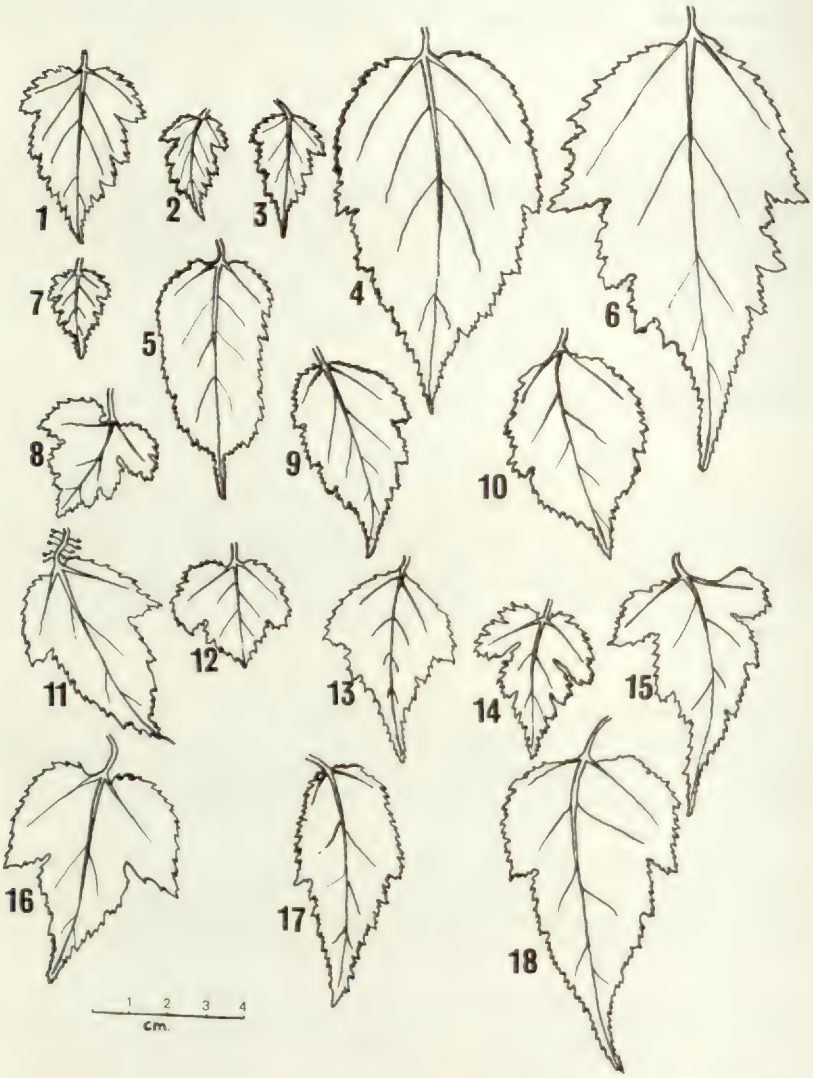


FIGURE 5. Leaves of **Neillia** species. 1. *N. sinensis* var. *sinensis* (*Wilson 701*); 2. *N. sinensis* var. *sinensis* (*Maire s.n.*); 3. *N. sinensis* var. *hypomalaca* (*Forrest 30475*); 4. *N. sinensis* var. *caudata* (*Fang 1057*); 5. *N. sinensis* var. *caudata* (*Cavalerie 2461*); 6. *N. sinensis* var. *villosa* (*Maire 2330*); 7. *N. sinensis* var. *rosea* (*Maire 1120*); 8. *N. sinensis* var. *ribesioides* (*Wilson 2382*); 9. *N. thibetica* (*Wilson 916*); 10. *N. thibetica* (*Chu 3611*); 11. *N. sparsiflora* (*Ten 461*); 12. *N. gracilis* (*Maire s.n.*); 13. *N. uekii* (*Russell 90*); 14. *N. lobata* (*Schneider 3558*); 15. *N. affinis* var. *affinis* (*Rock 22729*); 16. *N. rubiflora* (*Ludlow et al. 19288*); 17. *N. thyrsiflora* (*Yü 20199*); 18. *N. thyrsiflora* (*Henry 12275*).

Neillia rubiflora is closely related to *N. affinis*. It is also rather similar to *N. thyrsiflora*, which grows in the same area and with which it has been confused. It differs from *N. thyrsiflora* in the lack of multiple buds on the flowering shoots, in its less-branched (usually racemose) inflorescence, its adpressed-sericeous floral tube, and its entire stipules.

5. **Neillia gracilis** Franch. Pl. Delav. 1: 202. 1889; Vidal, Adansonia II. 3: 157. *pl. 2, fig. 2.* 1963. FIGURE 5: 12.

China. YUNNAN: Yangtze watershed, prefectural district of Likiang, eastern slopes of Likiang snow range, 4000 m., June 1922, *Rock 4422* (A, E); eastern flank of the Lichiang Range, lat. 27° 25′ N, 3000–3300 m., June 1910, *Forrest 6033* (E); eastern flank of the Lichiang Range, lat. 27° 12′ N, 3000 m., May 1906, *Forrest 2244* (A, E); at base of range to NW. of Ho Shui, 3300–4000 m., June 1906, *Forrest 1871* (E); paturages des mont derrière Tong Tchouan, 2600 m., *Maire 1100* (E); ibid., 1914, *Maire 559* (E); 27° 30′ N, 100° 45′ E. 2800 m., 25 May 1921, *Kingdon-Ward 3986* (E); Likiang snow range, 28 June 1939, *Ching 30281* (A); Likiang-hsien, 2800 m., July 1935, *Wang 70883* (A); Chungtien valley, 3500 m., 9 July 1939, *Feng 1936* (A); in cacuminis montis Tche-tchang prope Tong-tchan, 3 June 1882, *Delavay 249* (A, isolectotype); mountains S. of Lichiang nr. Hochin and Chinho, 25–28 May 1922, *Rock 4079* (A); Lichiang range, 31 July 1914, *Schneider 2071* (A); sine loc., 1937, *Yü 15282* (A). SZECHUAN: In declivibus graminosis regionis temperatae jugi Daörlbi medii inter Yenyuen et Yungning, supra vic. Hungga, 3500 m., 13 June 1914, *Handel-Mazzetti 2960* (E); inter Hunka et Woholo, 3000 m., 13 June 1914, *Schneider 1506* (A, E).

This species, *Neillia gracilis*, is the most distinct species of the genus, being suffrutescent and rhizomatous. In inflorescence and flower characters it resembles *N. affinis* var. *pauciflora* but differs in having only two ovules per carpel, a character it shares with *N. lobata* and *N. uekii*. *Forrest 1871* is a very robust variant, with the inflorescence forming a small panicle. In other respects this collection matches the rest of the material; it may perhaps represent a distinct variety.

6. **N. uekii** Nakai, Bot. Mag. Tokyo 26: 3. 1912; Vidal, Adansonia II. 3: 158. 1963. FIGURE 5: 13.

N. millsii Dunn, Kew Bull. **1912:** 108. 1912.

Korea. Prov. N. Heian, around Matan (Unsan), 28 June 1917, *Wilson 8714* (A); N. Heian, Kakai, 5 Aug. 1918, *Wilson 10587* (A); Prov. Pyengan, Yengben, 30 June 1937, *Mrs. R. K. Smith* (A); Prov. Pyengan, in dumosis Pyekdan, 12 June 1914, *Nakai 1774* (A); Kangkai, 6 Oct. 1909, *Mills 107* (K, holotype; A, isotype of *N. millsii*); in petrosis Pyongyang, June 1901, *Faurie 85* (A); in petrosis vallium Coreae mediae, July 1906, *Faurie 316* (A, E).

Neillia uekii is the only species of the genus known from Korea, where it is endemic. It is similar to *N. lobata* and *N. gracilis* in having only two ovules per carpel, but differs from all the species of the genus in having a sparse indumentum of tuberculate-based, stellate hairs on the branches in the region of the inflorescence. These hairs are ultimately deciduous,

but the tuberculate bases remain attached to the fruiting axis and are easily recognized. According to Vidal (*loc. cit.*), the name *N. uekii* was published in January 1912, whereas *N. millsii* was published in March of the same year.

7. **Neillia lobata** (Rehd.) Vidal, Adansonia II. 3: 157. *pl. 2, fig. 5.* 1963. FIGURE 5: 14.

N. longeracemosa Hemsl. var. *lobata* Rehd., Jour. Arnold Arb. 1: 257. 1920.

China. SZECHUAN: Inter Oti et Yungsin-hsien prope Quentin, ca. 2900 m., 4 June 1914, *Schneider 3558* (A, holotype; E, isotype); inter Tu-yung-pu et Yen-yuan-hsien, ca. 3000 m., 12 May 1914, *Schneider 4151* (A); in regionis temperatis inter oppidum Yenyuen et flumen Yalong, 27° 31′, fruticetis circa vicum Tsin-tienpu, ca. 2750 m., 12 May 1914, *Handel-Mazzetti 2218* (E).

Neillia lobata is allied to *N. uekii*, but differs in possessing more deeply lobed leaves, finely tomentose bark on the old wood, and in lacking the characteristic tuberculate-based stellate hairs of *N. uekii*. The Handel-Mazzetti specimen cited above is a very poor one, and some doubt must remain as to whether it actually is *N. lobata*.

8. **Neillia sparsiflora** Rehd., Jour. Arnold Arb. 1: 237. 1924; Vidal, Adansonia II. 3: 157. *pl. 2, fig. 1.* 1963. FIGURE 5: 11.

China. YUNNAN: Circa Pe-yen-tsin, Kou-ty, 1917, *Ten 462* (A, holotype; E, isotype); ibid., 1918, *Ten 531* (A, E).

A very distinct species, *Neillia sparsiflora* is characterized by the presence of long capitate-glandular bristles on the short shoots and petioles. It is closely related to *N. sinensis*, and is known from only three specimens: the two cited above, and a further one cited by Vidal (Yunnan, Djo Kou La près Pin Tchouan, vii 1907, *Ducloux 5348*, P).

9. **Neillia sinensis** Oliv. in Hook. Ic. Pl. 16: *t. 1540.* 1886.

As mentioned above (p. 142), this species and *Neillia thibetica* form an intergrading complex of forms difficult to separate into distinct taxa. However, six varieties are recognizable in *N. sinensis*:

1. Floral tube glabrous; leaves glabrous or pilose only on the veins beneath; short shoots glabrous or sparsely pilose.
   2. Stipules ovate-cordate, dentate; leaves large, usually little lobed, often caudate (pedicels 2–3 mm., glabrous; floral tube 1.6–2.5 times longer than broad). ..... var. *caudata.*
   2. Stipules oblong, oblong-ovate, or lanceolate, not cordate, entire or with 1 or 2 small teeth; leaves relatively smaller, often lobed, usually not caudate.
      3. Floral tube less than 6.5 mm. long (pedicels 2–5 mm., glabrous; floral tube 2–3 times longer than broad; flowers 15–19 in each inflorescence). ..... var. *ribesioides.*
      3. Floral tube more than 6.5 mm. long (pedicels 3.5–7 mm., glabrous;

floral tube (2–)2.5–4 times longer than broad; flowers 10–17 in each inflorescence). ..... var. *sinensis*.

1. Floral tube usually with sparse patent hairs near the base; leaves pubescent to pilose on the surface beneath, usually densely so; short shoots pubescent to pilose.
   4. Floral tube 5.5–6 mm.; pedicels up to 2 mm. ..... var. *rosea*.
   4. Floral tube 6.5 mm. or more; pedicels exceeding 2 mm.
      5. Stipules ovate-cordate; pedicels less than 3 mm. ..... var. *villosa*.
      5. Stipules oblong, not cordate; pedicels exceeding 3 mm. ..... var. *hypomalaca*.

Var. **sinensis** Vidal, Adansonia II. 3: 160. *pl. 2, figs. 7, 8.* 1963.

FIGURE 5: 1, 2.

China. SHENSI: Langchow, Kuan Shan, 2000 m., 3 July 1922, *Hers 2343* (A); Tai-pe-shan, 1910, *Purdom 1* (A, E); ibid., *Purdom 467* (A); Tu-kia-po, 4 June 1897, *Giraldi* (A). KWANGSI: Hang-on-yuen, woods, 10 June 1936, *Chung 81758* (A). HUPEH: W. Hupeh, May & Sept. 1907, *Wilson 86* (A, E); Hsing-shan-hsien, 1300–2000 m., June & Sept. 1907, *Wilson 189* (A, E); sine loc. *Henry 5554A* (A); sine loc. *Henry 5554B* (E); N. Tan-schian, Mar. 1912, *Silvestri 4589* (A); Paokang, 10–20′, *Wilson 701* (A, E). SZECHUAN: Sine loc. *Henry 5695* (A). YUNNAN: Wei-hsi plain, *McLaren D27* (A, E); Wei-hsi-hsien. Yeh-chih, 2400 m., July 1935, *Wang 67945* (A). HUNAN: Yünschan prope urbem Wukang, 600–1300 m., 6 June 1918, *Handel-Mazzetti 765* (A); ibid., *Handel-Mazzetti 12010* (E). KANSU: About Satanee and near Di-er-kan, *Farrer & Purdom 54* (E); ad fl. Tchiluco, 18 June 1885, *Potanin* (A).

Neillia sinensis var. *sinensis* is easily recognized by its long, narrow, glabrous floral tube, its few-flowered inflorescences and its long, glabrous or sparsely hairy pedicels. An extreme form is represented by *Wilson 189*, in which all parts are glabrous.

Var. **caudata** Rehd., Pl. Wils. 1: 436. 1913. FIGURE 5: 4, 5.

N. glandulocalyx Lévl., Fl. Kouy Tcheou 348. 1914–15; Vidal, Adansonia II. 3: 160. *pl. 2, fig. 6.* 1963.

N. thibetica var. *caudata* (Rehd.) Vidal, Adansonia 3: 164. *pl. 3, figs. 5, 6.* 1963.

China. YUNNAN: Mengtze, E. mt., 2000 m., *Henry 9669* (A, holotype); Yong-shan-hsien, 2100 m., 4 June 1932, *Tsai 50992* (A); Chen-hsiung-hsien, 1850 m., 3 July 1932, *Tsai 52706* (A); sine loc., *Tsai 51196 bis* (A). SZECHUAN: Nanchuan-hsien, 2100–2500 m., 27 May 1928, *Fang 1057* (A, E). KWEICHOW: Route de Pin Fa à Tou Yun, 25 July 1905, *Cavalerie & Fortunat 2461* (E, holotype and isotype of *N. glandulocalyx*; A, isotype); Top-kying, Ten-shan, Sunyi, 400 m., 4 June 1930, *Tsiang 5283* (A); Tuyun, Ma-tsoon-ling, 500 m., 11 July 1930, *Tsiang 5744* (A); She-won-san, Haufeng, 4 July 1936, *Teng 90524* (A). KWANGSI: Yang wu, Ling-chuan district, 21–30 July 1937, *Tsiang 27882* (A); Kon-Tung, Min-shan, N. Luchen, 1000 m., 18 June 1928, *Ching 6107* (A); Loh-hoh-tsien, Lin-yuin-hsien, Lao-shan slope, 1450 m., 20 May 1933, *Steward & Cheo 450* (A); Sze-hoh-tou, Lin-yuin-hsien, 12 Apr. 1933, *Steward & Cheo 172* (A); Ling-wan district, *Lau 28719* (A).

As explained above I prefer to treat var. *caudata* under *Neillia sinensis* (as it was originally described by Rehder), rather than under *N. thibetica*, where Vidal places it. It is a variable taxon, particularly in the lobing of the leaves, which may vary from quite deeply lobed, as in the type, to completely unlobed, as in some leaves of *Fang 1057*. Even on the same shoot, considerable variation in the degree of lobing may be found. The number of flowers per raceme is also variable.

The type of *Neillia glandulocalyx* (*Cavalerie & Fortunat 2461*) is a very poor fruiting specimen; however, in the Edinburgh herbarium there is a sheet labelled: "Flora of Yunnan, Yunnan-sen district [all this printed] *Cavalerie 2461*." This is a much better specimen, and appears to be a mislabelled duplicate of *Cavalerie & Fortunat 2461* (Mr. A. Lauener informs me that other, similar mislabellings are found in the Léveillé herbarium). On the basis of this specimen, which has both flowers and fruits, I am convinced that *Neillia glandulocalyx* and *N. sinensis* var. *caudata* belong to the same taxon; the distinctions between them noted by Vidal (number of ovules, leaf shape) are variable and are not, in my opinion, reliable for the separation of distinct species.

Var. **ribesioides** (Rehd.) Vidal, Adansonia II. 3: 161. 1963.

FIGURE 5: 8.

N. ribesioides Rehd. Pl. Wils. **1**: 435. 1913.

China. YUNNAN: Chao-tung-hsien, 2000 m., 19 May 1932, *Tsai 50929* (A). SZECHUAN: Pan-lan-shan, 2300–3000 m., June and Sept. 1908, *Wilson 2382* (A, holotype; see below); Tchen-keou-tin, *Farges 494* (E); Cheng-kou-hsien, 3 May 1932, *Fang 10315* (A).

The type sheet of this taxon poses a problem; I have seen three sheets labelled *Wilson 2382*, two at the Arnold Arboretum and one at Edinburgh. The holotype sheet (A) has two shoots on it. One of these, which has flowers with glabrous floral tubes, is marked "typical form," thus agreeing with a note with Rehder's original description: "Our specimen contains 2 branches, one with a glabrous calyx tube, which I consider the typical form . . ." The other shoot is, in general, rather hairier, the flowers have finely pubescent floral tubes, and there are more flowers in the inflorescence. All the specimens on the other two isotype sheets (A and E) match this second, hairier shoot on the holotype sheet. I regard this hairier shoot as being *Neillia thibetica*, and it is interesting to note that the preceding number, *Wilson 2381*, is clearly *N. thibetica*; this matches the hairy shoots on *Wilson 2382* very well. Is it possible that these specimens have become mixed at some stage, and that most of the plants labelled *2382* are really part of *2381*? The other specimens cited above match the typical *Wilson 2382* very well and are characterized by their short, glabrous floral tubes, glabrous pedicels, and small, rather deeply cut leaves, somewhat similar to those of the common British hawthorn (*Crataegus monogyna* Jacq.).

Var. **villosa** (W. W. Sm.) Cullen, comb. et stat. nov. FIGURE 5: 6.

N. villosa W. W. Sm. Notes Bot. Gard. Edinburgh **10:** 53. 1917; Vidal, Adansonia II. **3:** 161. *pl. 2, figs. 9–11.* 1963.

China. YUNNAN: Vicinity of Yunnan-sen, *Maire 2330* (E, holotype and several isotypes).

This taxon is essentially a densely hairy analogue of *Neillia sinensis* var. *caudata*; it has similar stipules and leaves and identical flowers. The indumentum of the leaves and short shoots is very dense, as it is also in the variety which follows.

Var. **rosea** Cullen, var. nov. FIGURE 5: 7.

A *Neillia sinensis* var. *sinensis* foliis subtus dense crispule pilosis, tubis floralibus brevissimis (5.6 mm.) differt.

China. YUNNAN: Vicinity of Yunnan-sen, *Maire 1120* (E, holotype and several isotypes); Kin-tchouy-chan, Lou-pou, coteaux, May–June 1922, *Maire* (E).

As *Neillia sinensis* var. *villosa* is the hairy analogue of var. *caudata* and var. *hypomalaca* that of var. *sinensis*, so var. *rosea* is that of var. *ribesioides*. It is characterized by its small, lobed leaves, very densely crisply pilose beneath, and its short, glabrous floral tubes.

Var. **hypomalaca** (Rehd.) Hand.-Mazz. Symb. Sin. **7:** 449. 1933; Vidal, Adansonia II. **3:** 161. 1963. FIGURE 5: 3.

N. hypomalaca Rehd., Jour. Arnold Arb. **13:** 337. 1932.

China. YUNNAN: Litiping range, Mekong-Yangtze divide, east of Wei-hsi, June 1923, *Rock 9171* (A, holotype; E, isotype); Tong-tchouan, collines, 2990 m., *Maire 429* (A, paratype); Du-long, halliers des mont, 2990 m., *Maire 529* (A, paratype); sine loc., 2900 m., *Maire 41* (A, paratype); Kangpu, Wei hsien, 1932 m., ravine, July 1935, *Wang 64159* (A); NW. Likiang, Lu-tien, 3 June 1939, *Ching 20483* (A); Pan Kiao Ho près Se'tsung, 17 May 1904, *J. B. Lo (Ducloux 633–E)*; Liu-ti-ping, 27° 12′ N, 3300 m., June 1917, *Forrest 13883* (A, E, WSY); Wei-hsi area, *Forrest 30475* (E); Mo-tsou, 600 m., June 1906, *Maire 387* (E); Tsekou, May 1912, *Mombeig 11* (E); San-o-chou, 2600 m., June 1913, *Maire 1108* (E); Kin-tchou-chan, 2900 m., May 1913, *Maire* (E); Ma-long, 2800 m., May 1913, *Maire 310* (E).

This variety is the hairy analogue of var. *sinensis*.

10. **Neillia thibetica** Bur. & Franch., Jour. Bot. Morot **5:** 45. 1891; Vidal, Adansonia II. **3:** 163. *pl. 3, figs. 1, 2.* 1963, excl. vars. FIGURE 5: 9, 10.

N. longiracemosa Hemsl. Jour. Linn. Soc. **29:** 304. 1892.

China. SZECHUAN: neighborhood of Tachienlu, 3000–4500 m., *Pratt 730* (K, syntype of *N. longiracemosa*); ibid., July and Sept. 1908, *Wilson 974* (A, E); ibid., 1924, *Cunningham 529* (E); ibid., 2600 m., Oct. 1910, *Wilson 4220a* (A); Pao-hsung-hsien, 2400 m., 20 June 1936, *Chu 2827* (E); ibid., 16 Aug. 1936,

Chu 3611 (E); Mupin, June and Sept. 1908, *Wilson 916* (A, E); ibid., 1600–2600 m., Oct. 1910, *Wilson 4220* (A); Ta-hsiang-ling, Ching-chi-hsien, June 1907, *Wilson 2381* (A, E); ibid., Ta Kwan, 2400 m., 7 Aug. 1939, *Chiao 1633* (A); Mapien-hsien, 29 May 1931, *Wang 23084* (A); sine loc., 1300–3000 m., *Wilson 3558* (A); Opien Hsien, 1500 m., 14 May 1932, *Yü 740* (A); Ta Hsian Ling, 2000–2500 m., 28 May 1922, *Smith 2078* (A).

As explained above, I have taken a different view of *Neillia thibetica* than Vidal. Of the specimens cited above, the most divergent is *Chu 2827*, which approaches *N. sinensis* in its long, narrow floral tube and rather long pedicels. However, in other features it is characteristic of *N. thibetica*, and it does not seem useful to treat it as a distinct variety.

The following specimens, because of their condition or the unsuitable stage at which they were collected, cannot be accurately identified. Possible names are suggested for some of them in parentheses at the end of the citations.

India. Khasia, *Maw* (A, probably *N. rubiflora*); Manipur, Ching Sow, 2600 m., Apr. 1882, *Watt 6532* (E); E. Bengal, *Hb. Griffith 2115* (A, probably *N. thyrsiflora* var. *thyrsiflora*).

China. YUNNAN: Ping Pien Hsien, 1400 m., 17 Apr. 1934, *Tsai 60254* (A, perhaps *N. thyrsiflora*); ibid., 27 June 1934, *Tsai 60483* (A); Wei-hsi-hsien, 2600 m., 16 Sept. 1934, *Tsai 57936* (A); between the Yangtze and Mekong, 2850 m., 29 Aug. 1915, *Handel-Mazzetti 7867* (E, *N. sinensis* var.); Atuntze, Doker-la, 3100 m., 4 Nov. 1937, *Yü 7855* (E); hills to the E. of Tengyueh, 2000 m., May 1912, *Forrest 7584* (E, *N. affinis* var.). SZECHUAN: Dailangshan, E. of Ningyueh, 2350 m., 24 Apr. 1914, *Handel-Mazzetti 1644* (E); sine loc., *Henry 5585* (E); Tien-chuan-hsien, 2300 m., 18 May 1936, *Chu* (E). SHENSI: Mt. Tou-pei-san, 20 July 1897, *Giraldi* (A, *N. sinensis* var.); Lungchan, Li-kia-po, 1800 m., 4 July 1922, *Hers 2370* (A). HUNAN: Yang-shan, Changning Hsien, 740 m., 13 July 1935, *Fan & Li 242* (A, *N. sinensis* var.).

NEILLIA IN CULTIVATION

Through the kindness of the owners and/or curators of many gardens, I have had the opportunity to survey the *Neillia* material in cultivation in Britain. Specimens of all the material sent to me are now in the herbarium at Liverpool University Botanic Gardens (LIVU–BG). A few specimens of cultivated plants were also included among the herbarium material studied. All this together shows that the following taxa are, or have been, in cultivation: *N. thyrsiflora*, *N. affinis* var. *affinis* and var. *pauciflora*, *N. uekii*, *N. sinensis* var. *sinensis* and var. *ribesioides*, and, *N. thibetica*.

A search through the relevant gardening literature shows no other taxa of *Neillia* reputed to be in cultivation, though of course, the name *longiracemosa* (= *thibetica*) is used frequently.

The following simplified key will serve for the identification of the cultivated taxa:

1. Leaves on flowering shoots with multiple, superposed buds; floral tube strigose; inflorescence usually a much branched panicle. . . . . *N. thyrsiflora.*
1. Leaves on flowering shoots with single buds; floral tube pubescent or glabrous, not strigose; inflorescence usually a raceme.
   2. Floral tube campanulate, as broad as or broader than long.
      3. Raceme elongate, the flowers 10 or more, spaced along the axis. . . . . *N. affinis* var. *affinis.*
      3. Raceme contracted, the 5–10 flowers fascicled at the ends of the branches. . . . . *N. affinis* var. *pauciflora.*
   2. Floral tube cylindric or cylindric-campanulate, longer than broad.
      4. Axis of inflorescence with tuberculate-based, stellate hairs; ovules 2. . . . . *N. uekii.*
      4. Axis of inflorescence glabrous or pubescent with simple hairs; ovules 3–9.
         5. Floral tube glabrous or with sparse patent hairs near the base; flowers 9–17(–21) in each raceme.
            6. Floral tube less than 6.5 mm. long. . *N. sinensis* var. *ribesioides.*
            6. Floral tube 6.5–10 mm. long. . . . . *N. sinensis* var. *sinensis.*
         5. Floral tube finely adpressed pubescent; flowers (19–)23–60 in each raceme. . . . . *N. thibetica.*

Neillia thyrsiflora D. Don

I have seen no recent material of this species, which according to Rehder was introduced in 1850. I have seen the following specimens:

Great Britain. R. H. S. Gardens, Wisley, as *Farrer 54*, from 7 acres, N. corner of long bed at W. side, 28 Aug. 1936, *Anon.* (WSY); ibid., N. border near Hornbeam towards W. end, 2 July and 27 Aug. 1937, *Anon.* (WSY). **Germany.** Botanischer Garten der Forstakademie, Muenden, Hanover, orig. Haage and Schmidt, Erfurt (sub *Spiraea*), 1873, *H. Zabel 86* (BH).

The Wisley plants have presumably both died, as neither was included in the living material sent to me from there. I have not seen any wild material under *Farrer 54* (see first specimen cited), but *Farrer and Purdom 54* is *N. sinensis*.

Neillia affinis Hemsl. var. affinis

Introduced in 1908, according to Rehder, but not widely distributed in gardens. I have seen living material from Kew, Cambridge, and Wisley; the Cambridge specimen was obtained from Kew (*fide* J. S. L. Gilmour *in litt.*) and was grown as *N. thibetica*; the Wisley specimen was grown as *N. ribesioides*.

Great Britain. R. H. S. Gardens, Wisley, 30 May 1950, *F. G. Meyer 3330* (BH); ibid., May 1934, *Anon.* (BH).

Neillia affinis Hemsl. var. pauciflora (Rehd.) Vidal

Another taxon apparently not grown today, but represented in the Wisley herbarium by the following:

Great Britain. R. H. S. Gardens, Wisley, from the W. end of 7 acres; 25 June 1941, *Anon.* (WSY).

This plant, which was grown as *N. longiracemosa*, and later identified as *N. thibetica* is of unknown origin; it may well have been grown from seed collected by Forrest.

Neillia uekii Nakai

Grown extensively at the Arnold Arboretum, introduced in 1906. I have seen living material from the Royal Botanic Garden, Edinburgh, and the following specimens:

United States. Arnold Arboretum, Jamaica Plain, Mass., 1 June 1926, *S. F. Blake* (NA–48213); ibid., 12 July 1918, *Schneider* (NA–48212); ibid., 21 June 1918, *Schneider* (NA–48211); ibid., 4 June 1936, *P. Russell 90* (NA–11465); ibid., 2 Sept. 1921, *G. M. Merrill* (BH). **Japan.** Kyoto city, 20 iv 1954, *Muroi 39* (A); ibid., 2 Aug. 1954, *Muroi 764* (A).

Neillia sinensis Oliv. var. sinensis

Introduced in 1901, this is the largest-flowered of all the species, though the smaller number of flowers makes it a less showy bush than good forms of *N. thibetica*. I have seen living material from the Royal Botanic Gardens, Kew, and the Royal Botanic Garden, Edinburgh, and the following specimens:

Great Britain. R. G. B. Edinburgh, from seed of *Wilson 189*, Edinburgh C642 (E); ibid., from seed of *Wilson 4220*, Edinburgh C87 (E). **United States.** Arnold Arboretum, Jamaica Plain, Mass., 5 June 1926, *S. F. Blake* (NA–48208); ibid., 9 June 1920, *Anon.* 6797–1 (BH); ibid., 20080–A, 22 June 1936, *E. Nilbending* (BH); ibid., A. A. 20080, 3 June 1936, *P. Russell 48* (NA–11433); ibid., 3 Aug. 1921, *G. M. Merrill* (BH); garden of B. Y. Morrison, Piney Branch Road, Takoma Park, Md., 13 May 1944, *B. Y. Morrison* (NA–161974, with photograph, Neg. 87983; BH); The Hickories, Cazenovia, N.Y., 20 July 1939, 5–6′, *S. R. Hafely* (NA–188174; BH); Bennington, Vermont, 4 June 1937, *E. T. & H. N. Moldenke 9696* (BH).

N. sinensis Oliv. var. ribesioides (Rehd.) Vidal

The only cultivated specimen of this taxon that I have seen is growing at Liverpool University Botanic Gardens, Ness. Its origin is unknown, but it is a large, spreading bush, obviously of considerable age. All specimens sent to me from elsewhere as *N. ribesioides* have proved to belong to some other taxon.

N. thibetica Bur. & Franch.

This is the species most frequently cultivated in Britain, and is probably the most attractive, especially in those forms with long, many-flowered racemes. It is frequently grown under the synonym *N. longiracemosa*. There is a good illustration of the plant as *t. 3* of the new series of the *Botanical Magazine*.

I have seen living material from the following gardens: R. B. G. Kew, R. B. G. Edinburgh, Chelsea Physic Garden, University of Exeter, Keillour Castle, University of Liverpool, University of London, R. H. S. Wisley, Messrs. Hilliers', Winchester; and the following specimen:

Netherlands. The Hague, Zuiderpark, 22 June 1956, *B. K. Boom 32240* (BH).

Several species of *Physocarpus* (which at one time was included in *Neillia*) may still be grown in some gardens as *Neillia*; the distinctions between the two genera are given in the introduction.

INDEX TO NUMBERED SPECIMENS CITED

Species are numbered 1–10, as in the revision; varieties are indicated by a, b, c, etc., in the order in which they are given in the revision.

Anderson 505: 1a.
Banerji 1210: 1a.
Cavalerie 2461: 9b.
Cavalerie & Fortunat 2461: 9b.
Cave 56: 1a; *97/47*: 4.
Chiao 1633: 10.
Ching 6107: 9b; *20483*: 9f; *30281*: 5; *81758*: 9a.
Chow 215: 9a.
Chu 2827: 10; *3611*: 10.
Chun 3795: 9a.
Cooper 556: 1a; *1229*: 1a; *2069*: 1a; *2814*: 1a.
Cowan 79: 4.
Cunningham 529: 10.
Delavay 249: 5.
Drummond 21043: 1a.
Ducloux 633: 9f.
Fan & Li 242: indet.
Fang 935: 3a; *1057*: 9b; *4694*: 3a; *10315*: 9c.
Farges 494: 9c.
Farrer 1757: 3a.
Farrer & Purdom 54: 9a.
Faurie 85: 6; *316*: 6.
Feng 1936: 5.
Forrest 554: 9f; *1871*: 5; *2244*: 5; *6033*: 5; *7584*: indet.; *7854*: 3c; *13883*: 9f; *14002*: 3b; *14342*: 3d; *17605*: 3d; *29567*: 3c; *29897*: 1b; *30023*: 3a; *30475*: 9f.
Gallatly 214: 1a.
Griffith 2115: indet.
Handel-Mazzetti 765: 9a; *1644*: indet.; *2218*: 7; *2960*: 5; *7867*: indet.; *8884*: 3a; *12010*: 9a.
Henry 5554A: 9a; *5554B*: 9a; *5585*: indet.; *5695*: 9a; *8968*: 3a; *9419* and *9419A*: 1b; *9669*: 9b; *10231A*: 3c; *12275*: 1a; *13653*: 1a.
Hers 2343: 9a; *2370*: indet.; *2965*: indet.
Howell 200: 3a.
Kingdon-Ward 1584: 3d; *3241*: 1a; *3986*: 5; *21135*: 1b.
Ko 55787: 1a.
Lace 2347: 1a.
Lau 28719: 9b.
Ludlow, Sherriff & Hicks 16520: 4; *19288*: 4; *20495*: 4.
Maire 41: 9f; *310*: 9f; *387*: 9f; *429*: 9f; *529*: 9f; *559*: 5; *1100*: 5; *1108*: 9f; *1120*: 9e; *2330*: 9d.
McLaren 27D: 9a.
Mills 107: 6.
Mombeig 11: 9f; *78*: 9f.
Nakai 1774: 6.
Pratt 347: 3a; *730*: 10.
Purdom 1: 9a; *467*: 9a.
Relzada 19034: 1a.
Rock 4079: 5; *4422*: 5; *7056*: 1a; *9171*: 9f; *22729*: 3a; *23275*: 3a.
Rohmoo Lepcha 766: 4.
Schneider 1506: 5, *2071*: 5; *3558*: 7; *4151*: 7.
Silvestri 4589: 9a.
Smith 1865: 3a; *2043*: 3d; *2078*: 10.
Steward & Cheo 172: 9b; *450*: 9b.
Sun & Chang 1234: 3c.
Ten 462: 8; *531*: 8.
Teng 90524: 9b.
Tsai 50929: 9c; *50949*: 3a; *50992*:

9b; *51041*: 10; *51196*: 9b; *52055*: 3a; *52706*: 9b; *56350*: 1a; *56895*: 1a; *57936*: indet.; *58432*: 1a; *59158*: 2; *60207*: 1a; *60254*: indet.; *60438*: indet.; *60717*: 1a; *62383*: 1a.

Tsang 27882: 9b.

Tsiang 5744: 9b.

Tu 272: 3c.

Wang 22992: 3a; *23084*: 10; *64159*: 9f; *65196*: 3a; *66940*: 1a; *67076*: 1a; *67945*: 9a; *68154*: 3b; *70883*: 5.

Wang & Liu 81820: 1a; *83503*: 1b.

Watt 6532: indet.

Wilson 86: 9a; *189*: 9a; *701*: 9a; *916*: 10; *916a*: 3; *974*: 10; *2380*: 3a; *2381*: 10; *2382*: 9c and 10; *3558*: 10; *3559*: 3a; *3560*: 3a; *4220*: 10; *4220a*: 10; *4886*: 3d; *8714*: 6; *10587*: 6.

Yü 740: 10; *941*: 3a; *7855*: indet.; *15282*: 5; *17115*: 3a; *17297*: 3a; *17974*: 1b; *19228*: 1b; *19409*: 1a; *20199*: 1a.

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I would also like to thank the owners or curators of many gardens (too numerous to mention individually) for their help in finding cultivated material; and finally, Dr. J. E. Vidal (Paris) for sending me a copy of his paper on *Neillia*; Mr. A. Lauener (Edinburgh) for help with Chinese place names and localities; and Mrs. K. Purcell (Ness) for preparing floral dissections.

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THE GENERA OF FAGACEAE IN THE SOUTHEASTERN UNITED STATES[1]

THOMAS S. ELIAS

FAGACEAE Dumortier, Anal. Fam. 11, 12. 1829. "Fagineae," nom. cons.

(BEECH FAMILY)

Deciduous to evergreen trees or shrubs of various habitats; sap watery; branches usually terete, slender, with numerous usually pale lenticels. Leaves with variable vernation, alternate [or verticillate in 3's], simple, occasionally distichous, petiolate, the blade entire, cleft or variously lobed, pinnately veined; stipules narrow, mostly deciduous. Plants monoecious [dioecious in *Nothofagus*]; flowers imperfect [rarely perfect]; inflorescences of pendulous to erect aments, or reduced spikes, heads, or cymules, or reduced to a solitary flower. Staminate flowers bracteate, the perianth with 4–8 imbricate lobes; stamens 4–20(–40); filaments filiform, free; anthers basifixed or dorsifixed, 2-loculate, the locules parallel and contiguous, dehiscence longitudinal, extrorse or introrse [a rudimentary gynoecium sometimes present]. Carpellate flowers subtended by an involucre (generally of many adnate and imbricate bracts) that partly or wholly incloses the fruit; perianth 3–8-lobed, uniseriate or biseriate, occasionally with rudimentary stamens; gynoecium 3–6-carpellate, syncarpous, with as many locules and styles as carpels; the style stigmatic along the upper surface, or stigma a terminal pore; ovary inferior and adnate to the lobed perianth, with 1 or 2 pendulous, anatropous, semianatropous or amphitropous, 2[1]-integumented ovules per locule, the ovules ± basal with one often aborting. Fruit a nut, usually 1-seeded by abortion, subtended by or inclosed in the muricate, bristly, scaly, or spiny involucre. Seed with a straight embryo, without endosperm, the cotyledons thick, fleshy, generally folded. Embryo sac development of the Polygonum type. Base chromosome numbers 12, 13. TYPE GENUS: *Fagus* L.

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. 39: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References which I have not seen are marked by an asterisk.

I am grateful to Dr. Wood for his thorough review of the manuscript and his numerous suggestions and additions in the course of this study. Dr. E. C. Abbe has kindly read the manuscript and has offered a number of useful and much-appreciated comments. Mrs. Nancy Dunkly has helped greatly in checking the bibliography and typing the manuscript. The illustrations are by Virginia Savage.

A family of eight genera and 400–500 species distributed throughout the temperate regions of the world, in mountainous tropical areas from Central America south to Colombia and the West Indies, and in Old World tropical areas, except tropical and southern Africa. Five genera are found in the continental United States, with *Fagus* L., *Castanea* L., and *Quercus* L. in our range. *Chrysolepis* Hjelmqv. is restricted to the Pacific coast region of the United States, and the chiefly Southeast Asian genus *Lithocarpus* Blume has a single species in California and Oregon.

The Fagaceae and the closely related Betulaceae (including Corylaceae) have generally been considered as constituting the order Fagales (Wettstein, Tippo, Rendle, Hutchinson). Current opinion among phylogenists is that the Fagales are derived from hamamelidaceous stock, which (fide Takhtajan) may serve as a link between the Magnoliales and the Amentiferae. Bessey, however, placed the Fagaceae with the Betulaceae and Juglandaceae and considered all three to be derived from a sapindaceous line. The Fagaceae have also been considered to have been derived from epigynous rosaceous stock (Berridge, 1914), but this view has not been accepted by later taxonomists. Hjelmqvist (1948), followed by Takhtajan (1969), preferred to place the Fagaceae and Betulaceae in separate but closely related orders. Cronquist (1968), in addition to including the Betulaceae and Fagaceae in the order Fagales, added the Balanopaceae. The affinities of this last family appear to be with the Fagales, but it should be studied further to determine its relationships more exactly.

Using evidence primarily from the carpellate inflorescences and fruit, Forman (1966) has postulated the lines of evolution of the cupules in the Fagaceae and has established intergeneric and specific relationships based on his findings. The basic structure of the carpellate inflorescence is considered to be a three-flowered dichasium (FIGURE 1). In the least specialized condition, each of the flowers and subsequent fruits is surrounded by several lobed involucres. In *Chrysolepis* the three trigonous fruits are enclosed by five free outer valves and two inner ones. From this condition it is supposed that the ancestral type had fruits that were trigonous (versus irregular or rounded) in section and that each of the three fruits of the basic dichasium was surrounded by three free valves, a condition that has not been found in any of the extant Fagaceae. Progressive specialization resulted in reduction in the number of involucral lobes and, later, fusion of the lobes to form the rounded cupular involucre found in *Quercus*, the C. *fissa* group of *Castanopsis*, and some species of *Lithocarpus*. Specialization was also accompanied by a reduction (by abortion) of the basic three-flowered dichasium to a single flower. The change from trigonous to ± irregular and/or to rounded fruits appears to have occurred concurrently with the reduction and fusion of the involucre.

These trends are illustrated diagrammatically in FIGURE 1 and are further noted under each of the three generally recognized subfamilies (cf. Oersted, 1871; Schwarz, 1936; Forman, 1964), which can be separated as follows:

Inflorescence of single- or many-flowered, axillary dichasial clusters. . . . . Fagoideae.
Inflorescence of aments of dichasial clusters or of solitary flowers.
Stigmas terminal, minute, punctiform; styles cylindrical; staminate flowers often with a rudimentary gynoecium; stamens usually 12; anthers minute, dorsifixed or versatile. . . . . Castaneoideae.
Stigmas on the inner surface of the generally flattened styles; staminate flowers without a rudimentary gynoecium; stamens usually 6; anthers large and ± basifixed. . . . . Quercoideae.

The subfamily Fagoideae includes only *Fagus* and *Nothofagus*. In *Fagus* the staminate flowers are in many-flowered heads, the carpellate dichasia lack the central flower of the basic three-flowered dichasium, and the styles are elongate and tapering, while in *Nothofagus* Blume the staminate flowers typically are in sessile to short-pedunculate one- to three-flowered dichasia, the central flower is always present in the carpellate dichasia, and the styles are short. That fruiting structures apparently have not evolved as rapidly as the floral parts, may be seen in the persistence of both free involucral valves and trigonous fruits. These tendencies are demonstrated in *Nothofagus*, some species of which exhibit the less specialized features, while others have more advanced characters, and many clearly show transitional features (cf. FIGURE 1). *Fagus* has 3(4)-colporate, suboblate-subprolate pollen grains, and *Nothofagus* has (4–)6(–7)-aperturate, oblate pollen grains.

Of the four genera in the Castaneoideae, only *Castanea* Mill. occurs in our range. The Old World *Castanopsis* Spach (approximately 110 species) is separated from *Castanea* mainly on floral and fruiting characters (see *Castanea*). Recently segregated from *Castanopsis*, *Chrysolepis* Hjelmqv. is distinguished by free involucral lobes and fruits (three per involucre) separated from each other by inner valves. *Lithocarpus* Blume (*Pasania* Oersted), including ca. 100 species distributed mainly in Malesia and the Pacific Islands and *L. densiflorus* (Hook. & Arn.) Rehd. in southwestern Oregon and in California, is distinguished by having each carpellate flower of a dichasium surrounded by its own involucre, which never shows vertical divisions or lobation. Langdon (1949) suggested several evolutionary trends in the floral structures in this subfamily, including a noticeable reduction in the inflorescence, apparently from a primary many-flowered dichasial type, and a reduction in floral members. There are also various transitional stages between hypogyny and epigyny that should be studied anatomically.

Forman (1966) concluded that reduction of the basic three-flowered carpellate dichasium to a single flower took place by suppression of the lateral flowers and that reduction by fusion of the four-valved cupule, first to a two-valved one and then to a single cup with no signs of valves, has occurred. The reduction of the individual flower-cupules within a dichasium is seen in *Lithocarpus* as eventually leading to a single flower and, consequently, a single fruit that closely resembles that of *Quercus*. This convergent evolution has led many workers to think that *Lithocarpus* and

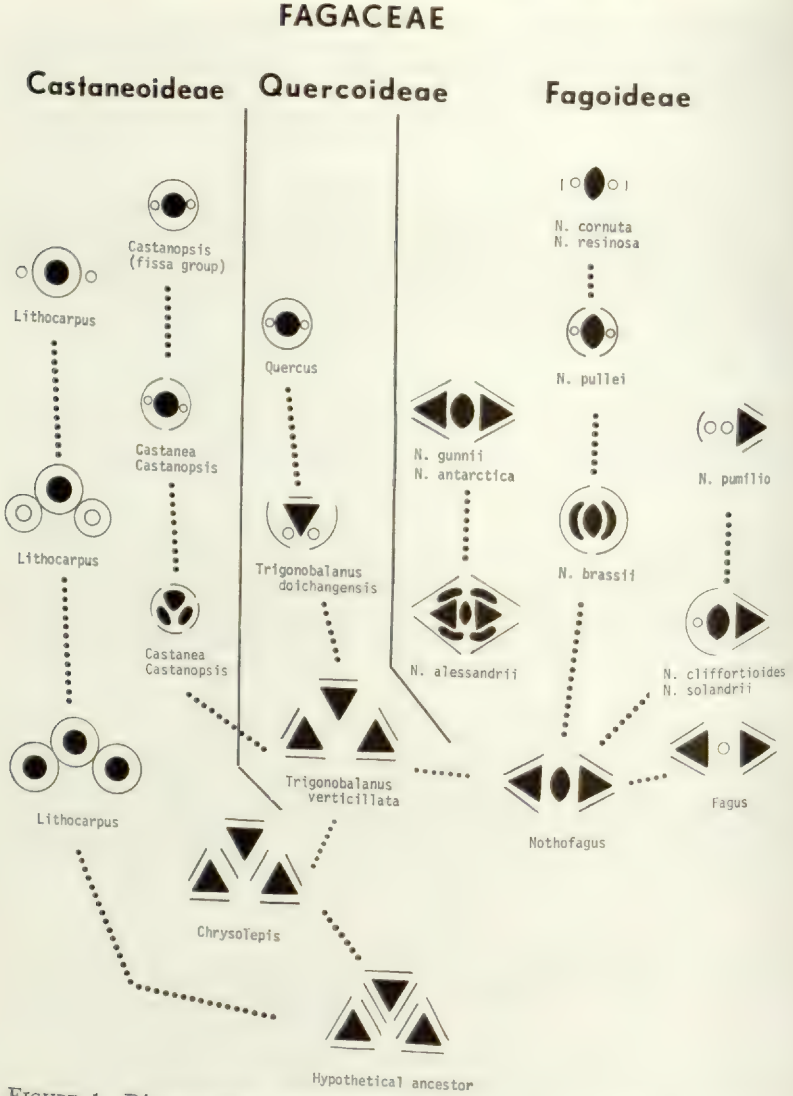

FIGURE 1. Diagrammatic scheme showing possible evolutionary relationships within the Fagaceae, based upon the involucre, flower number, and fruit shape. The basic carpellate inflorescence is considered to be a three-flowered dichasium. Shapes used indicate approximate shape of fruits in cross section, small undarkened circles represent abortive flowers, and lines inclosing fruits represent involucre. No attempt has been made to account for every variation found in the Fagaceae. Based mainly on Forman (1966) and van Steenis (1953).

Quercus are congeneric, but these workers have failed to consider the total biology of the two genera.

The reduction in the number of valves by lateral fusion is best seen

in *Castanea* and *Castanopsis*. A four-valved cupule, usually with three fruits is considered to have undergone fusion of the lateral valves to form a two-valved cupule, and, along with this, the number of flowers has been reduced to one per cupule. Further reduction can be seen in the "*fissa*-group" of *Castanopsis*, in which the two-valved cupule has given way to a completely fused, one-flowered cupule (cf. FIGURE 1).

The subfamily Quercoideae includes only *Quercus* (300–350 species) and the recently described *Trigonobalanus* Forman (2 species: *T. doichangensis* (A. Camus) Forman, of northern Thailand, and *T. verticillata* Forman, of Borneo and Celebes).

Evolutionary tendencies in the Quercoideae are toward a reduction of the carpellate clusters of flowers to either a pair of flowers or a solitary one; toward a change in shape and reduction of the number of fruits per cupule; and toward a reduction by fusion of the cupular valves to form a single valveless cupule. Forman (1964) considered *Trigonobalanus* to be less advanced than *Quercus* and perhaps close to the ancestral stock of the Fagaceae, an idea based primarily on the carpellate flowers, i.e., the flowers borne in clusters of 3(–7) as compared with the presumably derived condition of the paired or solitary carpellate flowers in *Quercus*. In addition, the 1–3(–7) trigonous fruits of *Trigonobalanus* are borne in a 3–5-valved cupule. In *Quercus*, a reduction of the flowers from 3 to 1 apparently has occurred, along with a change in fruit shape from triangular to round. Reduction of the cupule valves and their probable fusion to form the single valveless cupule of *Quercus* are further specializations.

Fagaceous remains (largely leaves and leaf fragments) have been recognized in the Upper Cretaceous, and these indicate that the family was once far more widespread than the extant members are.

The Fagaceae are of considerable economic importance. Members of this family, because of their abundance and very suitable wood, are one of the most important sources of hardwood timber. The wood, valued for its tough, hard, strong, yet attractive appearance, is used in various phases of construction, furniture making, and in quality tools. *Quercus Suber* L., cork oak, native to the Mediterranean region is the source of commercial cork. Edible nuts and, to a limited degree, lumber are obtained from *Castanea*. Species of *Fagus* are also used as lumber sources, and the beechnuts are highly sought after by various animals, both domestic and wild.

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KEY TO THE GENERA OF FAGACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Trees or shrubs with alternate, simple leaves with small usually caducous stipules; flowers unisexual; staminate flowers in erect or pendulous aments or heads, the perianth 4–8-lobed; carpellate flowers 1–4 in an involucre, the perianth 4–8-lobed, the ovary inferior, 3–6-loculate with 1–2 ovules per locule; involucre becoming indurated in fruit, lobed or entire; fruit usually a nut, 1-seeded by abortion; seed without endosperm.*

A. Staminate flowers in dense many-flowered, pendulous heads; the fruit triangular; germination epigeous; bark smooth; buds lanceolate, sharp-pointed. . . . . 1. *Fagus.*

A. Staminate flowers in erect to pendulous aments; the fruit subglobose, turbinate or variously compressed, never triangular; germination hypogeous; bark scaly or furrowed, usually rough; buds usually rounded, ovoid or ellipsoid.

B. Staminate flowers in erect aments; carpellate flowers borne on androgynous aments, the ovary 6(–9)-loculate, styles usually 6, stigmata terminal, minute, punctiform; involucre with fasciculate spines, inclosing usually 1–3 fruits, splitting into 2–4 valves at maturity. . . 2. *Castanea.*

B. Staminate flowers in ± pendulous aments; carpellate flowers borne separately, the ovary 3(4–5)-loculate, the styles generally 3, stigmatic on the inner surface; involucre cupuliform with numerous usually imbricate scales, partially inclosing the single fruit. . . . . 3. *Quercus.*

Subfamily FAGOIDEAE [Oersted]

1. **Fagus** Linnaeus, Sp. Pl. 2: 997. 1753; Gen. Pl. ed. 5. 432. 1754.

Deciduous trees of low or moderate elevations and generally moist habitats in temperate regions of the Northern Hemisphere; bark smooth, usually pale; wood hard, close-grained; branchlets terete with acute, often lustrous, chestnut-brown buds, the inner bud scales accrescent, marking the base of the branchlets with persistent ring-like scars. Leaves convex and plicate in vernation, deciduous [or persistent], usually dentate, coriaceous to subcoriaceous, petiolate; leaf-scars small, elevated, subelliptic, with marginal rows of minute vascular bundle scars; stipules linear-lanceolate, infolding the leaf in bud, fugacious or rarely persistent. Flowers vernal (shortly after the leaves unfold). Staminate flowers short-pedicellate, borne in globose, many-flowered heads (dichasia, fide Brett, 1964) on long drooping peduncles with (0–)2(3) bracteoles, the inflorescences arising from base of shoots of the year or from axils of their lowest leaves; perianth 4–8-lobed, the lobes imbricate in aestivation, ovate, rounded, with 8–40 stamens inserted on the base of the perianth; filaments slender, exserted; anthers basifixed, introrse, obtuse or sagittate at base; pollen 3(4)-colporate, suboblate to subprolate. Carpellate flowers in 2–4-flowered pedunculate clusters in axils of upper leaves of the year, sessile, surrounded by numerous awn-shaped hairy bracts, the outer bracts often bright red, longer than flowers, the inner shorter and united below to form a 4-lobed involucre; perianth urceolate, villous, with 4 or 5 linear-lanceolate acute lobes, the tube triangulate and adnate to the 3-locular ovary; styles 3,

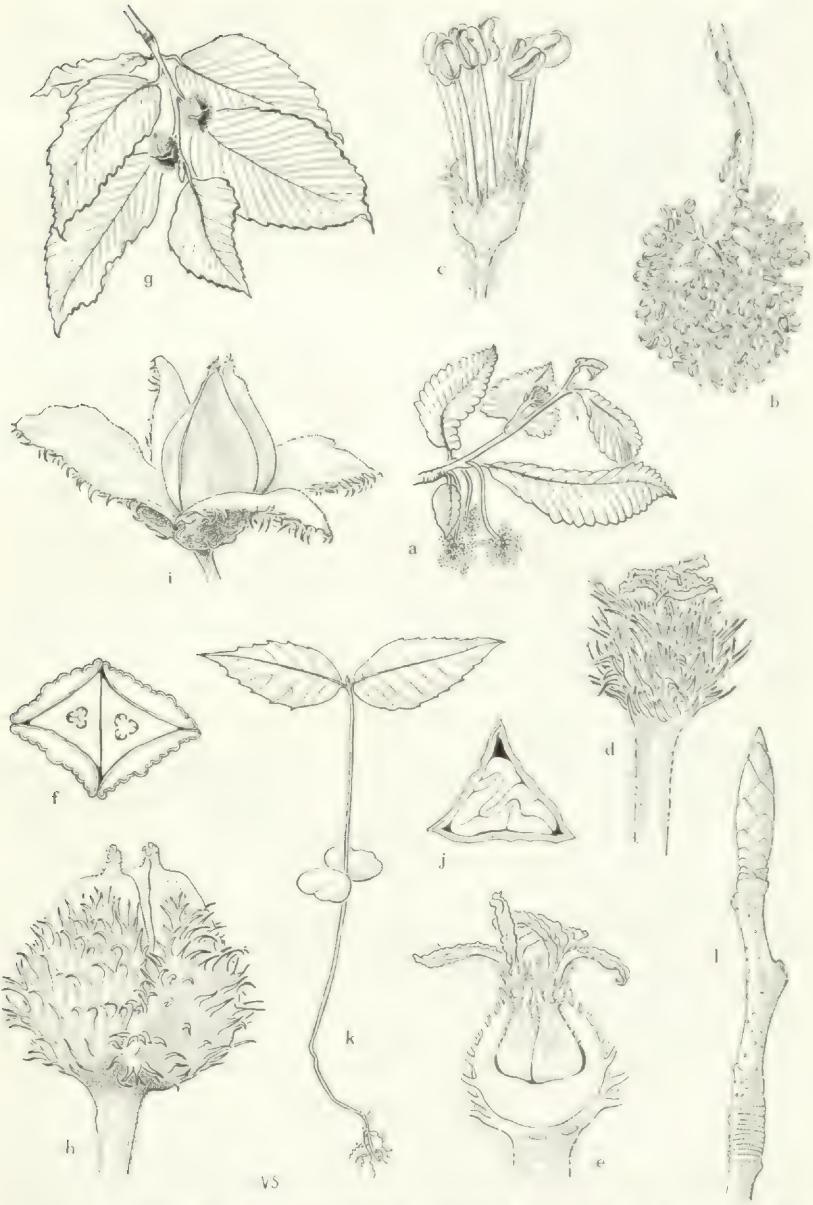


FIGURE 2. **Fagus.** a–l, *F. grandifolia*: a, flowering branchlet, × ½; b, staminate inflorescence, × 2; c, staminate flower, × 6; d, carpellate inflorescence, × 3; e, carpellate inflorescence with part of involucre removed to show flowers, × 4; f, carpellate inflorescence in semidiagrammatic cross section to show ovules, × 6; g, fruiting branchlet, × ⅛; h, involucre and two fruits, × 2; i, involucral bracts unfolding to show mature fruits, 1½; j, fruit in cross section to show cotyledons, × 2; k, seedling, × ½; l, winter twig showing bud, × 1½.

slender, recurved, pilose, exserted, becoming stigmatic toward the apex; stamens wanting; ovules 2 in each locule, suspended from apex of locule, amphitropous, the micropyle superior. Involucre (in fruit) becoming woody, pedunculate, ovoid to subglobose, covered with [sometimes glandular] stout, recurved prickles or tubercles, inclosing 2–4 fruits, ultimately separating into 4 valves. Fruits ovoid, unequally triangular, acute or winged at the angles, concave and longitudinally ridged on the sides, chestnut-brown and lustrous at maturity, rostrate (remnants of style); pericarp thin, of two closely united integuments, the inner membranaceous. Seed dark chestnut-brown, solitary, without endosperm; cotyledons thick and fleshy, plano-convex, plicate and ± united, sweet, oily; radicle minute, superior; germination epigeal. LECTOTYPE SPECIES: *F. sylvatica* L.; see Britton, N. Am. Trees 271. 1908. (Classical Latin name derived from Greek *phagein*, *to eat*, in reference to the edible nuts.) — BEECH.

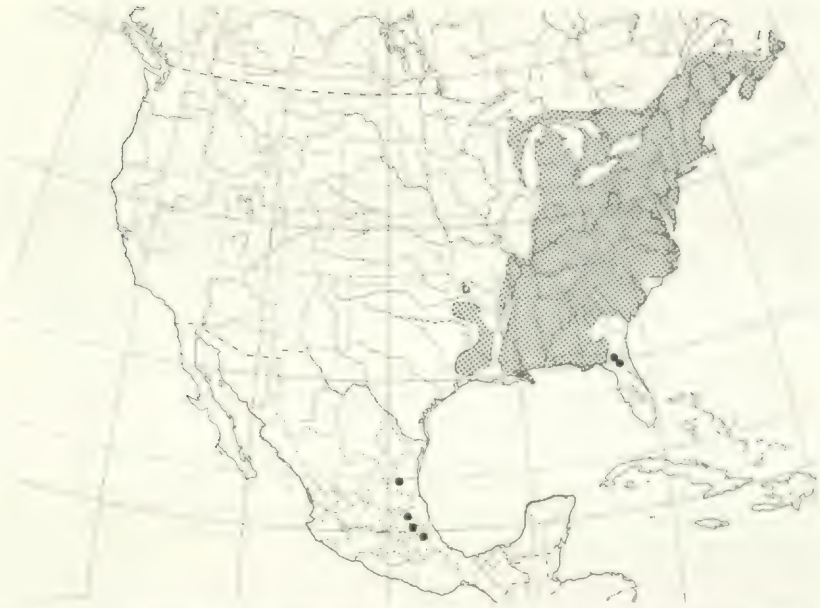
A genus of eight to ten species, represented in the southeastern United States by *Fagus grandifolia* Ehrh., $2n = 24$,[2] (*F. ferruginea* Ait., *F. americana* Sweet), which occurs from Cape Breton Island and Nova Scotia to Maine, southern Quebec and southern Ontario, northern Michigan and eastern Wisconsin, south to the Wabash and Mississippi River valleys in southern Illinois, southeastern Oklahoma, eastern Texas and eastward to northern Florida. (See MAP.) Varietas *caroliniana* (Loud.) Fern. & Rehd., distinguished by its darker leaves, which are often thicker, rounded or subcordate at the base, and smaller toothed, is found from Florida to Tennessee, north to southeastern Massachusetts, Ohio, Indiana, southern Illinois, and Missouri.

Fagus mexicana Martínez, known from four localities in the Sierra Madre Oriental in the states of Tamaulipas, Hidalgo, and Puebla, Mexico (see MAP), is probably best treated as *F. grandifolia* var. *mexicana* (Martínez) Little. The common orobanchaceous parasite of beech, *Epifagus virginiana* (L.) Bart., is scattered throughout the range of *F. grandifolia* and is also present in two of the Mexican populations, but is as yet unknown in Puebla. Since the dispersal mechanism of *Epifagus* is unknown, it is interesting to speculate on the spread of the parasite to or with the disjunct beech populations.

Fagus sylvatica L., $2n = 24$, often cultivated in the United States is widespread through much of Europe, and *F. orientalis* Lipsky occurs in the Caucasus region. The remaining species are found in central and southern China, Japan, and Korea.

Berry (1923) thought that *Fagus* originated in southeastern Asia and spread from there, becoming at one time pan-temperate as evidenced by the abundant fossilized material known from Europe, Russia, Japan, and the western United States. From a study of pollen from peat bogs, Sears found postglacial evidence that *Fagus* occurred farther west in the United States than the present limits of the genus. Numerous fossilized leaves in

[2] Aufderheide (1931) reported the haploid number of *F. grandifolia* as 6, but in view of later counts of $n = 12$, the $n = 6$ count must be considered questionable.



MAP 1. Present distribution of *Fagus grandifolia*. Distribution in United States mostly generalized; disjunct populations in Tamaulipas, Hidalgo, and Puebla, Mexico, are var. *mexicana*. Based mainly on Little in Fowells (1965) and Fox & Sharp (1954).

Europe from Miocene and Pliocene deposits have been attributed to the New World *F. grandifolia* by Tralau (1962). The present disjunct distribution of *Fagus* probably represents the remnants of a once widespread pan-temperate genus of numerous species.

Three series of populations of *Fagus grandifolia*, each with distinct ecological requirements, along with areas of introgression, were recognized by Camp (1951) but not given formal taxonomic status. The white beech, best seen in moist river valleys, is found in the southeastern and southern United States. Typically found on the well-drained southern Appalachian slopes on usually stabilized talus, the red beech extends from there northward to Canada. The northern gray beech is adapted to the cool, moist area at the southern edge of the northern coniferous forest and occurs southward at higher elevations than the red beech. It commonly occurs in pure stands above 650 m. in New England and Canada. A detailed ecological and/or biosystematic study of the three series is needed to determine not only the exact relationships of the various populations, but the status of var. *caroliniana* and var. *mexicana*.

Fagus grandifolia and *Acer saccharum* are the climax species in much of the deciduous forest formation from west of the Allegheny mountains to New York, Ohio, and Wisconsin. The shade-tolerant beech is often found in nearly pure stands in many areas within its range, e.g., higher

altitudes in the southern Appalachians (Russel, 1953). *Fagus* in our range is generally more abundant on the moister northern slopes and on soil with pH 4.1 to 6.0.

The anemophilous flowers appear in late April or early May, shortly after the leaves begin unfolding. Cross pollination is generally necessary for seed production, plants of most species of *Fagus* being moderately to largely self-sterile. Individual trees seem to show varying degrees of self-fertility in successive years, but this needs to be carefully studied and documented. Neilson & Schaffalitzky (1954) reported proterandry in *F. sylvatica* and *F. grandifolia* varying in degree with the weather, warm dry spring conditions resulting in shorter periods of proterandry. They found the stigmas of *F. sylvatica* to be receptive to pollen for approximately 10–14 days. Artificial hybrids between *F. sylvatica* (♀) and *F. grandifolia* (♂) were produced, the progeny showing intermediate leaf characters and some tendency toward hybrid vigor.

The fruits require only one growing season to mature and are shed when the first heavy frost causes the involucral valves to separate. Germination takes place in early spring to early summer of the following year. Seed production is somewhat sporadic, with good crops every two to three years. Dispersal is mainly by rodents or large birds. Although seed germination and seedling development are common in beech stands, vegetative reproduction by root suckers is often encountered. In open areas, beech trees develop a thick, short trunk with large, low spreading limbs and a broad, rounded crown. The thin, pale bark is very susceptible to fire injury and overexposure to sunlight (sunscalding).

A number of forms of *Fagus* are cultivated. Of these the copper beech, *F. sylvatica* f. *atropunicea* (Weston) Domin, is probably most frequently grown as an ornamental in the United States. Several of the Asian species are also cultivated to a limited extent in the Northeast. In New England and Canada, *Fagus grandifolia* is susceptible to attack by the beech scale insect, *Cryptococcus fagi*, which is soon followed by the fungus *Nectria coccinea* var. *faginata*. Several species of the fungus *Fomes* occur on the beech in our range.

The wood is hard, strong, and very close grained but not very durable. It is used in the manufacture of chairs and tool handles and is perhaps the principal wood used for clothespins (Strausbaugh & Core, 1953).

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Subfamily CASTANEOIDEAE Oersted

2. **Castanea** Miller, Gard. Dict. Abridg. ed. 4. 1: ord. alph. 1754.

Large to small, erect to spreading deciduous trees or shrubs of the temperate Northern Hemisphere, with large taproots and furrowed, brownish bark; branchlets terete, the terminal buds covered by 2 pairs of slightly imbricate scales, the outer pair lateral, the inner accrescent, becoming oblong-ovate and leaving narrow ringlike scars upon falling. Leaves convolute in vernation, elliptic to oblong-elliptic, the veins terminating at the tips of the usually coarse serrations, deciduous, petiolate; stipules paired, ovate to linear-lanceolate, acute at apex, scarious to herbaceous, infolding the leaf in bud, usually caducous; leaf-scars semioval, slightly elevated, with an irregular marginal row of small vascular bundle scars. Flowers in ± erect catkin-like staminate or androgynous racemes or spikes (false panicles fide Camus); staminate inflorescences ± erect, vernal (appearing with the unfolding of the leaves), borne in the axils of the lower leaves of the year; androgynous inflorescences usually erect, shorter than the staminate, borne in the axils of later leaves. Staminate flower subtended by a minute ovate bract; perianth deeply divided into 6 ovate lobes, the lobes imbricate in bud, slightly puberulous, pale stramineous, with 6–18 (–20) exserted stamens, filaments filiform, incurved in bud, free; anthers small, ovoid to subglobose, dorsifixed, introrse, 2-locular, with longitudinal dehiscence, pollen usually 3-colporoidate, prolate to subprolate; rudimentary ovary occasionally present. Carpellate flowers at base of androgynous inflorescences, sessile, solitary or 2 or 3 within an involucre of closely imbricate, pubescent to tomentose scales and ± branched spines; involucre subtended by a bract with two lateral bractlets; perianth urceolate, with 6 short obtuse lobes, pubescent, with 6–8 rudimentary stamens; styles usually 6 (–9), linear, spreading, pubescent below the middle, tipped by the minute punctiform stigmas; ovary incompletely (3–)6(–9)-loculate, each locule with 2 axile, collateral, semianatropous, and descending ovules. Involucre at maturity of fruit subspherical to oblong, pubescent and spiny on the outer surface, with elongated, ridged, branched spines fasciculate between the deciduous scales, inclosing 1–3 (rarely more) fruits, and splitting into 2–4 valves at maturity, the inner surface of the involucre with a lustrous pubescence. Fruits maturing in one season, ± ovoid and variously compressed, acute apically and beaked by the persistent perianth and styles, usually bright chestnut-brown and lustrous, with a large basal scar. Seed usually solitary, the abortive ovules borne apically; embryo straight, the cotyledons thick, fleshy, ± undulate and ruminate, inclosing remnants of endosperm between the folds, often sweet; germination hypogeal. Lectotype species: *Fagus Castanea* L. = *C. sativa* Mill.; see Britton, N. Am. Trees 271. 1908. (The ancient Latin name of the

FIGURE 3. **Castanea.** a–j, *C. pumila*: a, fruiting branchlet, × ½; b, staminate inflorescence, × 1; c, androgynous inflorescence, × 1½; d, staminate flower, × 10; e, carpellate flower, × 6; f, carpellate flower in semidiagrammatic longitudinal section showing two of the six locules, × 6; g, ovary in semidiagrammatic cross section, × 10; h, involucre with fruit, × 1; i, embryo with aborted ovules at the apex, × 2; j, seedling, showing large taproot, × ½.

European chestnut, derived from its Greek name, *kastanea* or *kastanos*.) — CHESTNUT.

About 12–14 species, widely distributed in eastern North America, southern Europe, northern Africa, southwestern Asia, central and northern China, Korea, and Japan. Characterized by having 6(–9) styles, the ovary 6–9-locular, the carpellate flowers borne at the base of androgynous catkins, the fruits maturing in one season, and the leaves deciduous, *Castanea* is closely related to the Old World *Castanopsis* (D. Don) Spach, which has three styles, the ovary three-locular, the carpellate flowers on separate catkins, the fruits maturing in two years, and the leaves persistent.

Dode (1908) divided *Castanea* into three sections: CASTANEA (§ *Eucastanon* Dode, BALANOCASTANON, and HYPOCASTANON, based on the number of fruits per involucre, the presence or absence of a persistent beak on the fruits, and their shape. Section HYPOCASTANON includes only *C. Henryi* Rehd., of China.

Section CASTANEA, including about six species with *C. dentata* (Marsh.) Borkh., $2n = 24$, American chestnut, in our range, demonstrates the disjunction shown by a number of relict Arcto-Tertiary genera between the eastern United States (*C. dentata*), southern Europe (*C. sativa* Mill., $2n = 24$), and southeastern Asia (*C. crenata* Sieb. & Zucc., $2n = 24$, *C. mollissima* Blume, $2n = 24$, *C. Seguinii* Dode, and *C. Davidii* Dode). Section CASTANEA is characterized by involucres each containing three fruits, rarely more, by the middle fruit being as wide as or wider than long, and by the fruits usually being conspicuously beaked.

Castanea dentata, formerly a dominant large tree in the eastern deciduous forest, ranges west from central Maine to New York, extreme southern Ontario, and southeastern Michigan, south to Ohio, southern Indiana, southern Illinois, western Kentucky, central Tennessee, northern Mississippi, Alabama, Georgia and northwestern Florida. Easily recognized by the large, oblong-lanceolate leaves which are coarsely serrate and by the very characteristic fruits, *C. dentata* can still be found throughout most of its original range in the form of stump sprouts that have been produced persistently for many years in spite of the attacks of the chestnut blight. The sprouts rarely reach flowering age, for usually when about 8–12 years old, they contract the blight and soon die (Neilstaedt, 1953). A few fruiting trees still survive in the wild, but most are in cultivation in areas isolated from the natural range of the species (cf. Thompson).

The natural replacement of *Castanea dentata* in the oak-chestnut forest of the eastern United States has been studied by several workers (cf. Keever, 1953; Nelson, 1955; Woods & Shanks, 1957, 1959). Replacement is mainly by species that were associated with *C. dentata* during its dominance. The main replacement species are *Q. rubra* L., *Q. Prinus* L., *Q. alba* L., *Acer rubrum* L., and *Liriodendron tulipifera* L. Although other tree species, many of which were subordinate to the dominant species of *Quercus* and *C. dentata*, can be found, this association is apparently becoming an oak-oak association.

Section BALANOCASTANON Dode, restricted to the eastern United States, has one (rarely two) fruit per cupule, the fruit longer than broad and usually beaked. The taxa of this section need careful study to determine their exact status. *Castanea ozarkensis* Ashe, Ozark chinquapin, a tree with gray, glabrous branchlets, leaves broadly lanceolate to oblong, coarsely toothed, minutely pubescent to glabrate beneath, the involucral spines pubescent, and the seed not flattened, is found in woods and on rocky slopes from Mississippi and Louisiana to Arkansas, Oklahoma, and southern Missouri. The closely related *C. pumila* Mill. var. *pumila*, $2n = 24$, Allegheny chinquapin, occurs in dry woods and thickets from New Jersey and eastern Pennsylvania, southwest to Tennessee, Arkansas, and eastern Texas, and east to Florida. The generally shrubby *C. pumila* can be distinguished from *C. ozarkensis* by the pubescent branchlets, the leaves oblong, serrate, whitish-downy beneath, the involucral spines pubescent and much longer than in *C. ozarkensis*. Varietas *Ashei* Sudw. (*C. Ashei* (Sudw.) Sudw.) found mainly on the Coastal Plain from northern Florida northward to southeastern Virginia, and westward to eastern Texas and Arkansas, has the clusters of involucral spines remotely arranged, leaving conspicuous open areas on the involucre. A third species, *C. alnifolia* Nutt. var. *alnifolia*, trailing chinquapin, found in Georgia, Florida, Alabama, and Mississippi, typically occurs in dry, sandy soils. Frequently spreading by underground rootstocks, var. *alnifolia* is a low, often trailing shrub. Varietas *floridana* Sarg. (*C. floridana* (Sarg.) Ashe, *C. Margaretta* (Ashe) Ashe), Florida chinquapin, is a small tree of upland woods, flatwoods, and hammocks in the Coastal Plain from North Carolina to northern Florida and westward to southeastern Louisiana. Kurz & Godfrey (1962) consider both this variety and *C. pumila* var. *Ashei* to be distinct species. *Castanea paucispina* Ashe, a poorly known plant described from eastern Texas (Newton County) and also attributed (fide Camus) to adjoining western Louisiana, is closely related to *C. alnifolia* but is separated from it by having a shorter, pubescent fruiting axis and the spines sparsely arranged on the involucre. *Castanea* × *alabamensis* Ashe, a hybrid of *C. dentata* and *C. alnifolia* var. *floridana*, occurs only in northern Florida. Another hybrid, *C.* × *neglecta* Dode (*C. dentata* × *C. pumila*) is of questionable status.

Although the species of *Castanea* are monoecious, cross pollination apparently is necessary for the production of viable seed. Solitary trees are frequently sterile, although the involucres may develop. A plausible explanation (which someone, hopefully, will prove or disprove) is that pollination may stimulate (chemically) the development of the involucre and ovary wall but that fertilization occurs only if the gametes are from another plant. Cross pollination is promoted by the staminate catkins maturing earlier than the androgynous catkins of the same plant. Clapper (1954) found that *C. mollissima* and *C. crenata* are self-sterile, but artificial hybrids between them show some self-compatibility. Self-sterility in *C. mollissima* was determined by McKay (1942) to be due to incompatibility, the pollen tube growing normally in cases of self-pollination,

but growth ceasing as the tube approached the egg, and no fertilization taking place. The two to three per cent fruit set was attributed to apomixis.

In a series of experiments to determine whether *Castanea* species are wind pollinated or insect pollinated, as suggested by some workers because of the rather conspicuous staminate spikes and the slightly odorous flowers, Clapper (1954) found them to be largely wind pollinated and concluded that this is more efficient than insect pollination and that insects are not essential for pollination. The stigmas were found to be receptive a few days after anthesis and most receptive 10–12 days after the beginning of anthesis. He also concluded that pollination was more effective in the morning than in the afternoon, apparently because of differences in humidity. From a series of interspecific crosses, it was determined that early flowering is dominant over late flowering.

Chestnut blight, caused by the ascomycete *Endothia parasitica* (Murr.) Anderson & Anderson, was first discovered in 1904 in the New York Zoological Park. Within 50 years it swept throughout the natural range of *Castanea dentata*, the species most susceptible to it. *Castanea sativa* is also proving to have little resistance against infection, but species of sect. Balanocastanon, as well as several species of *Quercus*, *Acer*, *Carya*, and *Rhus*, are susceptible in varying lesser degrees. The Asiatic species of *Castanea* show considerable resistance, but all serve as host to the blight fungus.

Following infection through a wound in the trunk or branches, the spores of *Endothia* germinate, and the mycelium rapidly spreads through the inner bark and cambium. Upon sporulation, a girdling canker (either appearing swollen or sunken) is usually formed, resulting in the death of the affected branch or the entire tree. Two types of spores are produced: relatively long-lived, one-celled, sticky, conidiospores produced during moist conditions, and larger, short-lived, two-celled ascospores. Conidiospores are spread by birds, insects, and to a lesser extent by rain, while ascospores are wind dispersed.

A very extensive breeding program was started soon after the devastating results of the chestnut blight became obvious. Breeding efforts were centered around *Castanea crenata*, the Japanese chestnut, and *C. mollissima*, the Chinese chestnut. Several disease-resistant hybrids have resulted, some suitable for commercial nut growing, others for ornamental trees. Clapper (1954) and Graves (1960, 1962) have presented techniques and results of some of the major breeding programs.

Castanea dentata was formerly an important timber tree in the eastern United States. The wood, brown, soft, light, open-grained, very durable, and easy to work, was widely used both indoors and in outside construction. The wood of *Castanea* species is high in tannin and was the major tanning agent for leather. Commercial chestnut growing in the United States has had to rely on Asiatic species and hybrids since the virtual elimination of the American chestnut.

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Subfamily QUERCOIDEAE Oersted

3. **Quercus** Linnaeus, Sp. Pl. 2: 994. 1753; Gen. Pl. ed. 5. 431. 1754.

Evergreen or deciduous trees or shrubs of varied habitats, often with astringent properties, the sap watery, the bark pale and scaly or dark and furrowed, the wood usually hard and close-grained or brittle and either diffuse or ring porous with both uniseriate and multiseriate rays, the pith star-shaped in section and continuous; branchlets slender, lenticellate, often fluted or ± prominently 5-angled; winter buds clustered at end of branchlets, the scales chestnut-brown, closely imbricate in 5 ranks, slightly ac-

crescent, caducous, leaving ring-like scars upon falling. Leaves usually with involute, convolute or revolute vernation, deciduous or persistent until spring or persistent for 2–4 years, simple, usually distinctly petiolate, the blade entire, variously lobed or dentate, often variable on the same branch, membranaceous to coriaceous, pinnately veined, the prominent primary veins extending to the margins or beyond as bristles, or veins anastomosing within; stipules obovate to lanceolate, scarious, often caducous, or those of the upper leaves occasionally persisting to the next year; leaf-scars slightly elevated, semiorbicular, usually broader than high. Flowers vernal, with or slightly after unfolding of leaves; staminate inflorescences in pendulous, fasciculate aments from axils of leaves of the previous year, from axils of the inner scales of the terminal bud, or from axils of leaves of the current year. Staminate flowers solitary or in clusters of 2 or 3, bracts absent or, if present, caducous; perianth campanulate, 3–6-lobed, usually divided to near the base; stamens (2–)4–12, inserted on a slightly thickened torus, the filaments free, filiform, exserted, the anthers usually ovate-oblong to subglobose, glabrous to rarely pubescent, 2-loculate, extrorse, pollen 3-colporate or 3-colporoidate, usually subprolate to prolate. Carpellate flowers solitary or in erect few-flowered spikes from the axils of the leaves of the current year, each flower inclosed by an involucre of many imbricate [or annular] scales, the involucre subtended by a caducous bract and 2 bractlets and later becoming the cupule of the fruit; perianth urceolate, with 6 short lobes, the perianth tube adnate to the incompletely 3(–4–5)-loculate ovary; styles usually 3, short or elongate, erect or incurved, often dilated above, stigmatic on the inner face or at the apex, usually persistent in fruit, stamens wanting [or abortive stamens as many as the lobes]; ovules 2 per locule, collateral, anatropous or semianatropous, descending. Fruit a nut (acorn) maturing in one or two growing seasons, ovoid, subglobose, or turbinate, usually short-pointed at the apex, generally 1-seeded by abortion, marked at the base by a large conspicuous circular scar; pericarp crustaceous or coriaceous, glabrous or with a pale tomentum on the inner surface, partially to completely inclosed in the accrescent cupule (involucre); cupule scales loosely or closely imbricate, flattened or variously thickened [rarely united into concentric rings], occasionally with a fringed margin. Seed with the aborted ovules at the base or at the apex, rarely lateral; cotyledons thick, fleshy, usually planoconvex and entire; often undulate on the back; radicle superior, included within the base of the cotyledons, hilum minute, basal or apical, germination hypogeal. $x = 12$. (*Quercus* Raf., *Cerris* Raf., *Scolodrys* Raf., *Macrobalanus* (Oersted) Schwarz, *Erythrobalanus* (Spach) Schwarz.) LECTOTYPE SPECIES: *Q. Robur* L.; see Britton, N. Am. Trees 278. 1908. (Classical Latin name for oak.) — OAK.

A genus of approximately 500–600 species in the mild-temperate regions of the Northern Hemisphere and in higher altitudes of the tropics, in the New World distributed southward to Mexico, Central America, and Colombia, and in the West Indies. In the Old World the genus is dis-

tributed from Manchuria, China, and Japan, southward to the East Indies and the Philippine Islands, and to southern India, westward along the Himalayas to western Asia, and through the Mediterranean region into western and northern Europe. It is absent from central and southern Africa, New Guinea, Australia, and the Pacific Islands. Approximately 30 species occur in the southeastern United States.

Although numerous infrageneric names of various ranks have been proposed for the American oaks by several workers, Trelease (1924) in his comprehensive treatment arranged them in three sections and more than 100 series. Three subgenera are recognized here: ERYTHROBALANUS (Spach) Oersted, restricted to the New World; QUERCUS (subg. *Lepidobalanus* (Endl.) Oersted) of both Old and New Worlds; and CYCLOBALANOPSIS (Oersted) Schneider, of eastern Asia. The differences between the two subgenera in North America are summarized in the following key.

Leaves entire or lobed, the lobes rounded or, if toothed, only mucronate-tipped, never aristate-tipped; styles short, abruptly flaring; acorns annual, cup scales usually prominently thickened basally and loosely appressed apically, acorn wall (pericarp) glabrous within; aborted ovules generally basal; bark usually soft gray and scaly, rarely black and deeply furrowed; wood pale, the larger vessels often plugged by tyloses, the smaller summer vessels thin-walled and rounded. ..... subg. QUERCUS.

Leaves entire or lobed, the lobes not rounded and, when toothed, aristate-tipped or, if entire, aristate-tipped from the veins; styles long, gradually flaring; acorns generally biennial, rarely annual, cup scales scarcely thickened basally and usually tightly appressed apically, acorn wall (pericarp) tomentose within; aborted ovules usually apical; bark rather hard, dark and furrowed, scarcely scaly; wood usually reddish, the vessels seldom filled with tyloses, the smaller summer vessels always thick-walled and rounded. . . subg. ERYTHROBALANUS.

Subgenus QUERCUS (*Lepidobalanus* Endl. ex Oersted; sect. *Lepidobalanus* (Oersted) Sargent; subg. *Macrobalanus* Oersted; *Macrobalanus* (Oersted) Schwarz; sect. *Leucobalanus* Engelmann; subg. *Leucobalanus* (Engelm.) Trelease) is represented in the eastern United States by approximately 16 species, many of which are confined to the Gulf Coastal Plain. The 57 series of subg. QUERCUS proposed by Trelease do not contribute significantly to an understanding of relationships and are not considered here, for the sections recognized by Rehder (1949) seem to represent more natural groups in this subgenus. Sections CERRIS Dumort., SUBER [Reichenb.] Spach, GALLIFERA Spach, and QUERCUS (§ *Robur* Dumort.) are confined to the Old World; our species are members of sects. ILEX and PRINUS.

Section ILEX Loudon, characterized by the evergreen habit; leaves usually entire, coriaceous; styles short, dilated toward the rounded apex; involucre with appressed scales; and fruit usually annual, is disjunctly distributed between the southeastern United States, southern Europe (*Quercus Ilex* L.), and southeastern Asia (*Q. phillyraeoides* Gray). Nearly restricted to the Atlantic and Gulf coastal plains, *Q. virginiana* Mill. extends from southeastern Virginia to southern Florida and western Cuba,

FIGURE 4. **Quercus** subgenus **Quercus**. a–d, *Q. Prinus*: a, staminate flower prior to anthesis, × 10; b, staminate flower at anthesis, × 10; c, stamen showing longitudinal dehiscence, × 20; d, carpellate flower, × 15. e–g, *Q. alba*: e, fruiting branchlet, × ⅓; f, mature acorn, × 1½; g, mature acorn in semidiagrammatic longitudinal section showing basally aborted ovules, × 1½. h, i, *Q. macrocarpa*: h, leaf, × ½; i, mature acorn, × 1. j, k, *Q. Muhlenbergii*: j, leaf, × 1;

and west to central and southern Texas and northeastern Mexico. Three varieties are recognized: var. *virginiana* (*Q. minima* (Sarg.) Small, *Q. pygmaea* (Sarg.) Ashe), var. *fusiformis* (Small) Sarg. (*Q. fusiformis* Small), and var. *maritima* (Michx.) Sarg. (*Q. maritima* (Michx.) Willd., *Q. geminata* Small, *Q. Rolfsii* Small, *Q. succulenta* Small).

Section PRINUS Loudon, with some 14 species in the United States, is distinguished by the deciduous, variously lobed to dentate leaves; the short styles, broad at the apex; the involucral scales appressed or rarely the upper free and subulate (*Q. macrocarpa*); and the annual fruit. The species that occur in our range include *Q. alba* L.; *Q. stellata* Wang., with var. *stellata* (*Q. Ashei* Sterrett, *Q. similis* Ashe), var. *Margaretta* (Small) Sarg. (*Q. Margaretta* Ashe ex Small, *Q. Boyntoni* Beadle), and var. *mississippiensis* (Ashe) Little (*Q. mississippiensis* Ashe); *Q. lyrata* Walt.; *Q. macrocarpa* Michx.; *Q. bicolor* Willd. (*Q. platanoides* (Lam.) Sudw.); *Q. oglethorpensis* Duncan; *Q. Chapmanii* Sarg.; *Q. Durandii* Buckl. (*Q. austrina* Small, *Q. sinuata* Walt.); *Q. Prinus* L. (*Q. montana* Willd.); *Q. prinoides* Willd.; and *Q. Muehlenbergii* Engelm. (*Q. Castanea* Muhl., *Q. acuminata* (Michx.) Sarg., *Q. Alexanderi* Britton, *Q. Brayi* Small). Approximately five species belonging here are found in the western United States, and four (perhaps more) species occur in eastern Asia.

Subgenus QUERCUS has fewer species (*ca.* 19) in Central America than subg. ERYTHROBALANUS. In both subgenera the Mexican species are poorly known, poorly represented in herbaria, and in need of careful study.

Subgenus ERYTHROBALANUS (Spach) Oersted (§ *Erythrobalanus* Spach, *Erythrobalanus* (Spach) Schwarz, § *Melanobalanus* Engelmann) is confined to the New World, mainly to the southern and eastern parts of the United States, Mexico and Central America. Trelease (1924) recognized 190 species (plus numerous subspecific taxa), which he distributed among 73 series, many of these with only one to three species! Muller (1942), in a taxonomic survey of the Central American species of *Quercus*, recognized many of Trelease's series, but he reduced to synonymy more than he recognized and, in addition, reduced many of the species described by Trelease. Since the series seem to be largely artificial, no attempt is made here to account for them. Muller concluded that the difficulties in delimiting subgeneric categories in subg. ERYTHROBALANUS lie in the poorly known Mexican species. For convenience, the species discussed here have been grouped mainly on the basis of leaf characters that do not necessarily reflect natural relationships. These relationships need to be worked out carefully.

Quercus chrysolepis Liebm., of southwestern Oregon south along the coastal ranges and the Sierra Nevada to northern Lower California and western Nevada, and *Q. tomentella* Engelm., of the California Channel Islands and Guadalupe Island off Baja California, are somewhat intermediate between subg. ERYTHROBALANUS and subg. QUERCUS. Both have

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k, mature acorn, × 1½. l, m, *Q. virginiana*: l, leaf, × 1; m, mature acorn, × 1½.

FIGURE 5. **Quercus** subgenus **Erythrobalanus.** a–e, *Q. ilicifolia*: a, branchlet with staminate inflorescences, × 1; b, staminate flower, × 12; c, carpellate flower, × 12; d, first year receptive carpellate flower in semidiagrammatic longitudinal section showing absence of ovules, × 20; e, mature acorn, × 1½. f–h, *Q. rubra*: f, second year carpellate flower in semidiagrammatic longitudinal section

entire persistent leaves that are involute in bud, usually 6–8 stamens, and abortive ovules that are basal or lateral. Although *Q. chrysolepis* was placed by Rehder in subg. QUERCUS, and some of its characters are intermediate between the subgenera, both species seem best referred to ERYTHROBALANUS because of the silky tomentum on the inner surface of the acorn wall and the biennial fruits.

Four other species, including *Quercus myrtifolia* Willd., of the southeastern Coastal Plain (southern South Carolina to southern Florida, west to southern Mississippi), have similar leaf characters but differ (as do the remaining species of the subgenus) in having 4–6 stamens per flower, styles finally recurved, and the abortive ovules apical. Almost grading into the above group are five species of the southeastern United States, commonly known as the willow oaks, which have mainly entire, but deciduous leaves. These are *Q. Phellos* L., *Q. incana* Bartr. (*Q. cinerea* Michx., *Q. brevifolia* (Lam.) Sarg.), *Q. imbricaria* Michx., and *Q. pumila* Walt. Formerly thought to be a distinct species, *Q.* × *laurifolia* Michx. (*Q. hemisphaerica* Bartr., *Q. hybrida* (Chapm.) Small, *Q. obtusa* (Willd.) Ashe, *Q. rhombica* Sarg.) has recently been considered by Burk (1963) to be the hybrid of *Q. Phellos* and *Q. nigra*.

The other species of subg. ERYTHROBALANUS have deciduous, variously lobed leaves (except some *Quercus nigra* L. and *Q. ilicifolia* Wang.) that are convolute in bud. An almost complete gradation in lobing can be found from one species to another, from an entire leaf to a slightly three to five lobed (apically) leaf, to those with five shallow lobes, and eventually to those with five to nine to eleven deep lobes. Entire to three lobed leaves can be found in *Q. nigra* L. (*Q. microcarya* Small) and *Q. ilicifolia* Wang. (*Q. nana* (Marsh.) Sarg.), while slightly three to five lobed, usually obovate leaves are generally evident in *Q. marilandica* Muenchh. (*Q. neo-ashei* Bush), *Q. arkansana* Sarg., *Q. laevis* Walt. (*Q. Catesbaei* Michx.), and *Q. georgiana* Curtis. The leaves of *Quercus falcata* Michx., including var. *falcata* (*Q. triloba* Michx., *Q. elongata* Willd., *Q. digitata* (Marsh.) Sudw.) and var. *pagodifolia* Ell. (*Q. Pagoda* Raf., *Q. pagodifolia* (Ell.) Ashe, *Q. leucophylla* (Ashe) Ashe) show a condition that continues to the more deeply lobed leaves of *Q. coccinea* Muenchh.; *Q. velutina* Lam. (*Q. missouriensis* (Sarg.) Ashe); *Q. palustris* Muenchh.; *Q. ellipsoidalis* Hill; *Q. Shumardii* Buckl., with var. *Shumardii* (*Q. Schneckii* Britton) and var. *texana* (Buckl.) Ashe (*Q. texana* Buckl.); *Q. Nuttallii* Palmer; and *Q. rubra* L. (*Q. borealis* Michx. f., *Q. maxima* (Marsh) Ashe). In the United States, the entire-leaved species of *Quercus* occur mainly in the southern United States, and there appears to be a trend toward the more lobed condition in the northern portions of the range of the genus.

Muller (1942) recognized 27 species as belonging to this subgenus in

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showing ovule formation, × 8; g, second year carpellate flower in semidiagrammatic cross section, × 25; h, mature embryo showing apically aborted ovules, × 1½. i, j, *Q. imbricaria*: i, mature leaf, × ½; j, mature acorn, × 1½. k–n, *Q. nigra*: k, l, m, variation in mature leaves, × ½; n, mature acorn, × 1½.

Central America (from Chiapas, Mexico, through Panama). *Quercus Humboldtii* Bonpl., the southernmost of the American species, is found from Panama southward into the Colombian Andes. The taxonomy of the species of subg. ERYTHROBALANUS in Mexico is very poorly known, perhaps due to the paucity of fruiting collections.

Hybridization among species of *Quercus* has been known and discussed for many years. Numerous hybrids have been described, but only relatively recently has the critical study of the true nature of the putative hybrids been begun. Natural, usually fertile, hybrids between recognized species of *Quercus* are common, but the total number of hybrid combinations is uncertain, for several species (e.g., *Q. rubra*) are polytypic, and some recognized forms may prove to be only variants of a polytypic species. Palmer (1948) listed what he considered to be 75 certain hybrids and approximately 15 dubious ones. Muller (1955) questioned the actual existence of so many hybrids, for many were based on minor variations that probably fall within the variability of the supposed parental species. Unfortunately, many hybrids described between 1900 and 1950 were based primarily on a few specimens with no attempt to provide quantitative data supporting the putative hybrids.

It has been clearly shown that the species that are compatible and produce fertile hybrids are the more closely related ones. Although all species of *Quercus* counted have $2n = 24$, natural hybridization between species of the subgenera QUERCUS and ERYTHROBALANUS is unknown and not expected to be found, although Pjatnitzky (1946) was able to cross experimentally *Q. Robur* with *Q. borealis maxima* [= *Q. rubra*] and *Q. macranthera* with *Q. borealis maxima* and produce vigorous seedlings.

Hybrid individuals or populations are usually found in areas where the ranges of two species overlap or where they once overlapped but now do not. Muller (1953) demonstrated that *Q. Havardii* Rydb. (confined to deep sandy soils) and *Q. Mohriana* Buckl. (on limestone) will only come into contact where erosion of the sandy areas exposes the limestone. Hybrids are readily produced but are confined to soils composed of a mixture of sand and limestone. Several other studies have also shown that hybrids are better suited to "hybrid" habitats than to the edaphic conditions of either parent. Hybrids between two allopatric species whose ranges now do not overlap, *Q. macrocarpa* Michx. and *Q. Gambelii* Nutt., were interpreted by Maze (1968) to have occurred during a period in the past when the two species were partially sympatric. Pleistocene migration was believed responsible for the sympatry.

Some species of *Quercus* in our range are sympatric with others of the same subgenus but have not yet been shown to hybridize with them. Among these are *Q. pumila*, *Q. myrtifolia*, *Q. Chapmanii*, *Q. Nuttallii*, and *Q. oglethorpensis*. Whether the apparent absence of hybrids is due to insufficient study or whether these species are incompatible with others remains to be seen, but the former appears to be more likely.

Flowering is vernal, the flowers appearing shortly before, with, or shortly after the new leaves. The staminate inflorescences usually develop from

axillary buds of leaves of the previous season. Development of the staminate inflorescences of *Q. alba* is initiated in early summer (late June); the inflorescence initials overwinter and then complete development the following spring. In contrast, the solitary or paired carpellate flowers are borne in the axils of the leaves of the current season. In *Q. alba* the carpellate flower primordia do not appear until late summer or early fall, overwinter, and mature the following spring as the terminal bud expands.

The lightweight pollen, produced in enormous amounts and a major contributor to pollen allergies, is dispersed by wind. Sharp & Chisman (1961) reported that the mature anthers of *Q. alba* open or close, depending upon the relative humidity, high humidity and rain often delaying or reducing pollen shedding and dispersal and, consequently, lowering acorn production. The staminate inflorescences are sensitive in varying degrees to freezing temperatures and prolonged dry winds. Nearly complete pollen dissemination requires as little as a few hours in some of the shrubby oaks and as long as several days in the larger tree species. Although not sufficiently studied, individuals of the various species of *Quercus* are cross-pollinated, for the plants are partially or wholly self-sterile.

In subg. Quercus, pollen-tube development and subsequent fertilization usually occur soon after pollination. In *Q. alba*, and presumably other species, pollination occurs before the ovules are completely developed. Syngamy may be delayed for a month or more in *Q. alba* (Turkel *et al.*, 1955) depending on the time of maturation of the ovule. Following fertilization, one of the six ovules (the other five abort, basally) develops along with the other parts of the carpellate flower into a mature acorn in one season. Pollination and pollen-tube development also occur in the spring in subg. Erythrobalanus, but fertilization in most species does not occur until the following spring. At the time of pollination, the ovules have not differentiated, and the entire ovary is rather undeveloped. By late spring, the ovule and placenta develop meagerly, but most of the development takes place the next spring. Fertilization of one of the ovules (the other five abort, usually apically) occurs approximately a year after pollination and the acorn matures in the fall of the second year.

Acorns of subg. Quercus generally require little or no dormancy and germinate soon after falling, if suitable environmental factors are present. The acorns of most species (temperate) of the subg. Erythrobalanus appear to require a period of dormancy before germinating the following spring. Germination in both subgenera is hypogeal, the fleshy cotyledons remaining inside the pericarp. Polyembryonic acorns with two or very rarely three embryos per fruit, are known in *Q. Prinus*, *Q. alba*, *Q. rubra*, and *Q. Robur* and probably occur in many more species of *Quercus*. The embryogeny of *Q. Robur* and *Q. velutina* follows the onagrad type but with very irregular cleavage. The bitegmic ovule is crassinucellar. The formation of short branches in the pollen tubes of *Q. Robur* is noteworthy.

Oaks are the most abundant trees over most of the eastern United States and in parts of the southern forest. The most extensive association is the oak-hickory (*Quercus-Carya*) forest found through much of the

Piedmont and Inner Coastal Plain of the Atlantic States, the Gulf Coastal Plain, and westward to eastern Texas and north throughout most of the Mississippi River Valley (Shelford, 1963). Various combinations of oak and hickory species occur throughout the association, the most frequent species being *Q. alba* L., *Q. rubra* L., *Q. velutina* Lam., *Q. stellata* Wang., *Q. marilandica* Muenchh., and *Carya cordiformis* (Wang.) Koch, *C. ovata* (Mill.) Koch, and *C. laciniosa* (Michx. f.) Loud. Braun (1950), restricting the oak-hickory forest to the Interior Highlands, centered mainly around the Ozark and Ouachita mountain region, preferred to label the remaining area as the oak-pine forest, emphasizing the sometimes transitory, sometimes persistent nature of the pines in the southeastern United States. Bourdeau (1954) attempted to determine why certain species of *Quercus* are found in some oak-hickory associations but not in others. He found that *Q. alba*, *Q. velutina*, and *Q. rubra*, generally restricted to mesic upland areas, are eliminated from drier, more rocky areas because their seedlings are not very drought resistant. They are, however, more shade tolerant than *Q. marilandica* and *Q. stellata*, which are restricted to the thin, rocky soils with periods of drought and considerable exposure.

Other associations include the *Liriodendron-Quercus* forest found in the northeastern United States, the maritime live-oak forest usually found in a narrow band along the coastline where dune areas have become relatively stable (cf. Bourdeau & Oosting), and the oak-chestnut forest of the eastern United States formerly found in our range throughout much of the Appalachian Mountains.

Vegetative reproduction is of considerable ecological importance in semiarid regions, which are often unsuitable for seedling establishment (Muller, 1951). Clonal thickets are formed by rhizomatous branches in several species of *Quercus* (*Q. Hinckleyi* Muller, *Q. Havardii* Rydb., *Q. pyrenaica* Willd., *Q. Ilex* L., and *Q. virginiana*). The dwarf *Q. pumila* also spreads in this way. Muller considers the resulting increase in longevity to be an important factor in the ability to compete with the more xeric forms.

Far too many species of *Quercus* have been described from fossil leaf fragments. Apparently the first identifiable oaks are found in Upper Cretaceous deposits. The leaves of the earliest oaks were entire, toothed, or scarcely lobed. Since deeply lobed leaves comparable to those of many species of subg. ERYTHROBALANUS appear much later in the fossil record, this condition is probably derived in *Quercus*. The relationship between *Quercus* and the fossil genus *Dryophyllum* is clouded with misidentifications and the lack of a comprehensive paleobotanical study of the two genera. Berry (1923) thought that *Quercus* probably diverged from ancestral *Dryophyllum* stock at the end of the Lower Cretaceous or the beginning of the Upper Cretaceous.

The oak wilt disease, caused by a heterothallic ascomycete, *Ceratocystis fagacearum* (Bretz) Hunt, is a serious menace that spread rapidly from the Midwest to the eastern and southern United States. The disease usually appears in the uppermost branches of the tree and spreads down-

ward to the trunk and roots. Wilting is caused by the great production of tyloses that block the xylem vessels, but toxins are also produced and may be the ultimate cause of death. Large masses of hyphae can be found on the outer surface of the sapwood and on the inner surface of the bark. Asexual reproduction is by conidia and sexual by ascospores from perithecia. The disease is spread by root grafts of trees growing close together or by the asexual or sexual spores being carried by insects. Most, or perhaps all species of *Quercus* are susceptible, those of subg. ERYTHROBALANUS apparently more so than species of subg. QUERCUS. Insect damage often is a serious threat and has been shown by Nichols (1968) to be the main cause of mortality of *Q. Prinus* and *Q. alba* in Pennsylvania. Heart rot, frequent in trees following fire damage, often makes the wood useless for lumber.

Quercus is extremely important in the hardwood lumber industry, mature oaks being among the larger hardwood trees and yielding a hard, tough, yet durable, resilient and elastic wood that is used in heavy construction, shipbuilding, and in better furniture. Of the two subgenera, QUERCUS typically has harder, stronger and more durable wood than the species of ERYTHROBALANUS, in which the wood is softer, more porous, and more open-grained. The more important timber species of subg. QUERCUS include *Q. alba*, *Q. macrocarpa*, *Q. stellata*, *Q. montana*, *Q. Prinus*, *Q. Garryana*, and *Q. bicolor*; those of subg. ERYTHROBALANUS include *Q. borealis*, *Q. velutina*, *Q. coccinea*, *Q. palustris*, *Q. laevis*, *Q. phellos*, *Q. texana*, and *Q. imbricaria*. *Quercus virginiana* reportedly has the hardest, strongest, and toughest wood of all oaks and is highly prized. As early as the 19th century the United States government was making concerted efforts to insure that adequate supplies of *Q. virginiana* would be available for naval stores. The decrease in shipbuilding demands, extensive cutting, the slow growing nature of the species, and the restricted range limit the usefulness of *Q. virginiana* as a lumber source.

Acorns have been used as a food supplement and as forage for animals, especially hogs. Among the best species of *Quercus* utilized are *Q. alba* and *Q. virginiana*, the former species used by the American Indians in making flour. Species of subg. QUERCUS generally have a low tannin content in the acorns and, consequently, are more readily edible than those of subg. ERYTHROBALANUS, which have to be leached to remove the high tannin content to make them suitable for human consumption. All acorns are high in carbohydrates.

Quercus Suber L., native to the Mediterranean region of southern Europe and the source of commercial cork, has been introduced into the southeastern United States, where cork growing has hardly been successful commercially. This species is also an excellent ornamental shade tree, as are a number of other oaks, including the Japanese *Q. myrsinifolia* Blume and *Q. glauca* Thunb., of subgen. CYCLOBALANOPSIS, both of which are evergreen trees grown to a limited extent in the warmer parts of our area. As with other members of subg. CYCLOBALANOPSIS, the cupule with the scales connate in concentric rings is characteristic.

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THE STAPHYLEACEAE IN THE SOUTHEASTERN UNITED STATES [1]

STEPHEN SPONGBERG

STAPHYLEACEAE Lindley, Syn. Brit. Fl. 75. 1829, nom. cons.

(BLADDERNUT FAMILY)

A small family of debated phylogenetic position comprised of five [2] woody genera with a total of ca. 50–60 species characterized by opposite [or alternate] compound [usually odd-pinnate] or trifoliolate [rarely simple] leaves and caducous stipules. Flowers perfect [or polygamous, rarely imperfect and the plants dioecious] in drooping panicles [or racemes], the perianth of 5 imbricated sepals and 5 petals with both series often connate at the base [sometimes connate into a tube]. Stamens 5, alternating with the corolla lobes and inserted either on or below the disk; pollen [di- or] tricolporate [or polyrugate]. Gynoecium [2– or] 3(4)-styled with a superior [2– or] 3(4)-locular ovary partially embedded at its base in a hypogynous disc [if present]; carpels with numerous apotropous crassinucellar ovules usually in two rows, placentation axile. Fruits capsules [drupes or berries]; seeds with endosperm. Represented in our area by the type genus, *Staphylea* L.

Divided into two subfamilies by Pax (1897), the Staphyleoideae is characterized by opposite leaves, carpels not united their entire length, capsular fruits, and wood with bordered pits. It includes the eastern Asian *Euscaphis*, the North Temperate *Staphylea*, and the tropical and subtropical *Turpinia*. The subfamily Tapiscioideae, consisting of *Huertea*, endemic to Peru and the West Indies, and *Tapiscia*, of eastern Asia, is distinguished by an alternate leaf arrangement and sometimes simple

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator, Carroll E. Wood, Jr.). The present treatment follows the plan initiated in the first contribution of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area dealt with includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. Material included in the descriptions in brackets applies to species outside this area, and references marked by an asterisk have not been seen by the author.

The illustration was drawn by the late Dorothy H. Marsh, with the addition of the seed and embryo by A. D. Clapman and Miss Virginia Savage, respectively. Appreciation is extended to Dr. R. B. Channell of Vanderbilt University who sent living materials for the illustration. I am most grateful to Dr. Wood for his ready advice and instructive help in the preparation of the manuscript and to Mrs. Nancy Dunkly for checking the bibliographic citations.

[2] A sixth genus, *Triscaphis* from Indo-China, has been referred to the Staphyleaceae by Gagnepain. Van Steenis (1960) states that this genus is either anacardiaceous or sapindaceous, not staphyleaceous.

leaves, connate carpels that develop into drupes or berries, and wood with simple pits. It has been suggested that the subfamilial traits and other differences, which include a distinct pollen morphology (a polyrugate type), would justify treating the Tapiscioideae as a separate family.

Placement of the family has been problematic since the Staphyleaceae appear to have affinities with several groups. Historically, the conflicting views have centered around placement of the family in either the Celastrales (De Candolle, Wettstein, Rendle, and Bessey) or the Sapindales (Reichenbach, Bentham & Hooker, Engler, and Hutchinson). More recently, Takhtajan (1959) has considered the Staphyleaceae to be a primitive member of the Sapindales. Cronquist (1968), although placing the family in the Sapindales, does not consider it ancestral to the order despite its many primitive features. Foster (1933), because of the similarities of the cytological aspects of *Acer* and *Staphylea*, concluded that the Staphyleaceae could have had a common origin with the Aceraceae. Heimsch (1942) concluded on the basis of his anatomical studies that the Staphyleaceae did not belong in the Sapindales but might best be placed in the Celastrales.

As indicated in the previous treatments of the genera of the Celastrales and Sapindales in the southeastern United States (Brizicky, 1963, 1964) the Staphyleaceae are thought to belong to the Cunoniales (or Saxifragales *sensu lato*) as advocated by Hallier (1908, 1912) and supported by van Steenis (1959, 1960). This alignment was first suggested by Lindley (1835) who based his genus *Ochranthe* on a species which was later transferred to *Turpinia*. Likewise, *Kaernbachia* Schltr. was described as a new genus in the Cunoniaceae but has been shown by van Steenis (1959) to be based on two additional species of *Turpinia*. The evidence for the placement of the Staphyleaceae with the Cunoniaceae hinges not only on the strong morphological resemblances (which are well outlined by Hallier, 1908, and van Steenis, 1960) but also consists of anatomical similarities (van Steenis, 1959). The admittedly scant embryological data summarized by Davis (1966) would also seem to be in accord with this placement. On the basis of distributional evidence, van Steenis (1960) has pointed out that the genera of the family "represent a marked northern counterpart to the Cunoniaceae which is largely a southern hemisphere family." Speaking of such antipodal pairs, he continues, "The meeting point of the areas of each pair and their overlapping margins are almost always found in the vicinity of the tropical zone. It would seem that the birthplace of these pairs must have been the tropics from which their ancestors have been branched off with a northward and southward directed distribution, respectively giving way to a subsequent development (diversity) in antipodial [sic] centres."

Although the placement of the Staphyleaceae in the Cunoniales seems to be the most reasonable alternative, this position should be considered tentative until further studies employing modern techniques have been made. Such a study might well include investigations of *Sambucus*

and *Bischofia* (cf. Airy Shaw, 1967; Webster, 1967, p. 312), which also seem to have affinities with the Staphyleaceae.

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1. **Staphylea** Linnaeus, Sp. Pl. 1: 270. 1753; Gen. Pl. ed. 5. 130. 1754, "Staphylaea."

Deciduous shrubs, rarely attaining treelike stature with terete branches, the pith terete; bark becoming gray to black and somewhat mottled. Leaves ± decussate, trifoliolate [or pinnately compound], the rachis finely pubescent (in ours), becoming glabrate; lateral leaflets subsessile, often becoming distinctly petiolulate; blades ovate to elliptic, about twice as long as wide, with a prominent midvein; the base oblique or obtuse, margins serrulate, the apex cuspidate; finely to densely pubescent (in immature material), the density greatest along the midrib and at the base; stipules linear, extra-petiolar, membranaceous, with ciliate margins, leaving distinct scars that become obscure at older nodes; rhachis with two small, stipule-like glands near the insertion of the petiolules and (in immature material) two obscure glandlike stipels at the base of each leaflet. Anthesis in spring [flowers appearing before the foliage and on second year wood, or] the panicles partially obscured by the immature foliage of that year's growth; each pedicel of a panicle with a pair of stipule-like bracts at its point of attachment to the peduncle, and with a swollen area at about the middle point of its length which appears to be a point of disarticulation. Calyx partially united at the base, only slightly shorter than the [pink or] cream-colored petals. Stamens inserted below the disc; filaments pubescent [or glabrous] below, exserted from the perianth at anthesis; anthers 2-loculate, longitudinally dehiscent and 2-lobed below the point of filament attachment; pollen binucleate when shed. Styles 3(4), free for most of their length but connate at the expanded, blunt stigmatic apex; ovary pubescent [or glabrous], partially embedded in the disc, 3(4)-loculate. Fruit an inflated, membranaceous, indehiscent capsule, the carpels usually separating from one another at the apex during maturation to yield a 3-beaked, 3-lobed, ellipsoid to obovoid brownish fruit. Seeds brown, subspherical, somewhat flattened, with a hard, impervious seed coat developed from the outer integument and a thicker, inner porous layer developed from the inner integument; endosperm fleshy; embryo straight with flattened cotyledons. Embryo sac of the Polygonum type. Base chromosome number 13. LECTOTYPE SPECIES: *S. pinnata* L.; see N. L. Britton, N. Am. Trees 637. 1908. (Name an abbreviated form of *Staphylodendron* [Tournefort], from Greek, *staphyle*, a raceme or cluster, and *dendron*, tree.) — BLADDERNUT.

A genus of nine or ten species with a disrupted arcto-Tertiary distribution in the North Temperate Zone of both the Old and New worlds; one species native in our area, one or possibly two additional species native

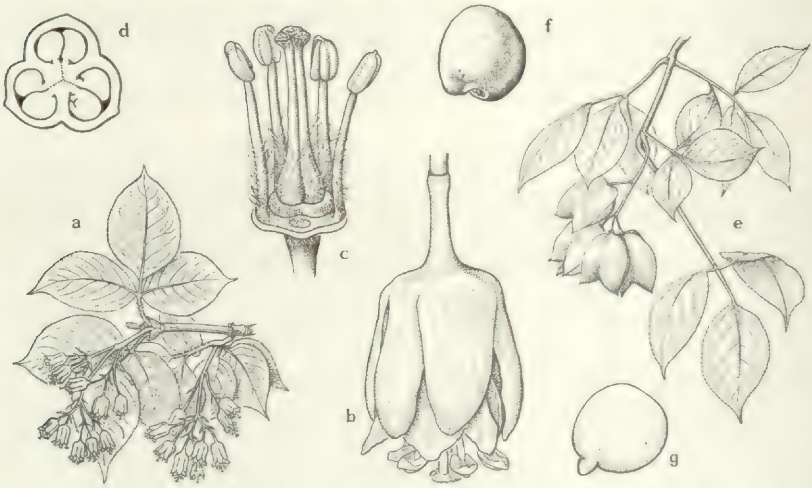

FIGURE 1. **Staphylea.** a–g, *S. trifolia*: a, branch with immature foliage and drooping panicles, × ½; b, individual flower with swollen area of pedicel and two-lobed anthers, × 4; c, same, perianth parts and one stamen removed—note pubescent filaments and ovary partly embedded in the disc, × 5; d, semi-diagrammatic cross section of three-loculate ovary with apotropous ovules in two rows, × 10; e, branch with mature foliage and immature, inflated capsules, × ¼; f, seed, × 3; g, embryo with disc-shaped, flattened cotyledons, × 3.

to the New World, several infrequently cultivated. *Staphylea trifolia* L., a small shrub becoming arborescent in the southern part of its range (up to 6 m. high and 15 cm. in diameter), is usually found growing in alluvial or limestone soils in the understory of deciduous forests and in thickets along stream banks, in moist ravines or on the shores of lakes and ponds. The species ranges from southern Quebec and Ontario to Minnesota, southward through eastern Nebraska and Kansas to Oklahoma, Arkansas, Tennessee, extreme northeastern Mississippi, and northern Alabama (along the Tennessee River) and Georgia. According to a report cited by Krause (1942), it was once known to grow in the vicinity of Alexandria, Louisiana. In our area it is primarily a species of the Piedmont, extending into the mountains or onto the Coastal Plain in only a few scattered localities.

Staphylea trifolia differs from the Californian *S. Bolanderi* A. Gray, endemic to the lower altitudes of the Sierra Nevada, primarily in its pubescent ovary and anther filaments. *Staphylea Pringlei* S. Watson, described from Nuevo León, Mexico, is doubtfully distinct from *S. trifolia*. *Staphylea Emodi* Wallich, of the northeastern Himalayas, appears to be closely allied to *S. trifolia*. Additional trifoliolate Asian species include *S. holocarpa* Hemsley, of central China; *S. Bumalda* DC., indigenous to central and western China, the mountains of Japan, and Korea; and *S. Forrestii* Balf. f. and *S. shweliensis* W. W. Sm., both of western China. Other species may be yet undescribed from this region. *Staphylea*

colchica Stev. is native to the southern Caucasus, while *S. pinnata* L. is distributed throughout Central Europe east into Asia Minor. Both have pinnately compound leaves. Their reputed hybrid, *S. elegans* Zobel, known only in cultivation, is the only hybrid reported for the family.

Brown (1944) recorded *S. splendens* (Berry) Brown from the Eocene Wilcox Flora of Tennessee but noted that *S. acuminata* Lesq. from the Florissant beds of Colorado more closely resembles *S. trifolia*. The presence of *Staphylea* in the Wilcox Flora, as well as other fossil floras, may give support to van Steenis's hypothesis of a tropical origin for the genus.

The wood of *Staphylea* is a relatively primitive diffuse-porous type with scanty paratracheal parenchyma and vessel elements with many-barred scalariform perforations and spiral thickenings in the walls. The wood rays are heterogeneous, tracheid or fiber-tracheid fibrous elements are present, and the phellem is derived directly from the epidermis. The stomata, of the cruciferous type, are confined to the lower surfaces of the leaves.

The few chromosome numbers recorded for the genus are the only counts available for the family. *Staphylea Bumalda* and *S. pinnata* are diploids with $2n = 26$, while *S. colchica*, a tetraploid, has $2n = 52$, and *S. trifolia* is a hexaploid with $2n = 72$. Foster (1933) observed secondary pairing in meiotic figures from pollen-mother-cells of *S. trifolia*, and Sax (1938) found that stomatal density decreases with increased ploidy level in these cytologically known species.

Little is known about either the breeding system or the pollination ecology of species of *Staphylea*, but entomophilous pollination seems to be the rule. The flowers of *S. trifolia* are proterogynous and adapted to long-tongued insects. The hypogynous disc surrounding the ovary has been reported to be nectar secreting. The number of capsules developed per inflorescence seems to be small in comparison with the number of flowers, and ovule abortion seems to be great and seed set small. Each locule typically contains between four and twelve ovules in *S. trifolia*, but Harris (1911b) found that of 12,072 fruit locules examined 47 per cent lacked seeds, while of those in which seed matured, 93 per cent contained only one or two seeds. The low percentage of seed set has been used as an argument for the presence of self-incompatibility and the necessity for cross-pollination, but the biological basis of the observed facts remains unknown. Shrubs of *S. trifolia* often occur in dense colonies that have been generally assumed to result from root suckering.

Its inflated, bladdery fruits are quite variable both in size and degree of apical lobing, and Harris (1912) found a positive correlation between fruit length and the number of seeds per locule. The capsules remain on the shrubs after the leaves have fallen in late autumn, making the colonies conspicuous during the winter months. Both the capsules and the individual seeds of *Staphylea* are buoyant, perhaps in adaptation to water dispersal. Ridley (1930) also suggested that the light weight of

the fruits may allow for wind dispersal. Seeds of *S. trifolia* have been germinated after scarification and freezing (Dore, 1962).

None of the species of *Staphylea* has any reported economic use other than as a garden ornamental. It has often been suggested that these shrubs should be more widely planted because of their pleasing flowers, interesting fruits, and shade tolerance.

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WHAT IS THE PRIMITIVE FLORAL STRUCTURE OF ARALIACEAE?

RICHARD H. EYDE AND CHARLES C. TSENG

"THE GENERA OF Araliaceae that are most remote from Umbelliferae are *Plerandra*, *Tetraplasandra*, and their near relatives; in general, these are the genera that are distinguished by a greater number of stamens or carpels. In an arrangement where the Umbelliferae follow the Araliaceae, one would have to place these genera at the beginning of the family. Since we can observe within the Araliaceae a very gradual transition from species with many stamens and carpels to those characterized by 5 stamens and 2 carpels, it is not improbable that we have here a reduction series and that the forms placed at the beginning of the generic sequence also represent the oldest types of the family." (Harms, 1894, p. 21, 22.)

"A few of the Araliaceae have ten or more petals, stamens, and carpels in a regular, symmetrical arrangement. These polymerous types have sometimes been regarded as primitive within the family, but they more probably have undergone a secondary increase in the number of parts of each kind. Pentamerous flowers are here regarded as primitive in the family and order." (Cronquist, 1968, p. 278.)

The first quotation, translated rather freely from Harms's monograph of the Araliaceae, cautiously expresses a view that has long prevailed concerning floral evolution in the family. H.-L. Li, in his revision of the Chinese Araliaceae, put it more emphatically. Of *Tupidanthus*, he wrote: "Its primitiveness . . . as indicated by the numerous stamens, ovary-cells, and styles, is unquestionable." Baumann-Bodenheim (1955), a leading student of fruit structure in Araliaceae and Umbelliferae, recognized a five-stage reduction series from the many-carpellate ovary to the pseudomonomerous ovary. As far as we know, Cronquist is the first author to question the "unquestionable" primitiveness of the polymerous flower in this alliance.

Ordinarily, primitive floral characters might be sought in genera with primitive wood characters; experience shows such an association of characters occurs fairly often. However no wood anatomist has yet carried out a thorough investigation of the Araliaceae, and the limited data available suggest no simple relationship between floral characters and xylem

characters. The most detailed observations to date (Rodriguez, 1957) show advanced xylem characters in temperate herbs (*Aralia californica*, *A. hispida*) and in the vine *Hedera helix*, where one would expect to find specialization, but primitive xylem characters such as scalariform perforation plates and heterogeneous rays are distributed among genera that differ greatly with respect to numbers of floral parts. Of course, future work on the wood anatomy of Araliaceae may reveal correlations with floral structure that are not now apparent. It should be kept in mind, however, that at least some of the Araliaceae have evolved through repeated radiation on oceanic islands, radiation apparently accompanied by complex changes in growth habit (e.g., trees to shrubs and back to trees again; *see* Carlquist, 1965, p. 191). If such changes were sufficiently widespread, the usual trends of wood evolution might be difficult or impossible to find in this family.

Since associated xylem characters are not presently of value for assessing the evolutionary status of polymerous flowers, we looked for an association between vascular characters — more specifically, vascular characters of the gynoecium — and the number of floral parts. One basic tenet of evolutionary plant morphology is that flowers with sepals, petals, stamens, and carpels united in various ways have evolved from flowers with all appendages free. Similarly, a flower in which all of the principal vascular bundles are separate is more primitive than one in which the principal bundles are variously united. In a group with inferior ovaries, the degree of union between dorsal carpel bundles and peripheral bundles (supplying epigynous appendages) may differ in different taxa, thus providing an indication of evolutionary advancement (Eames & MacDaniels, 1947, *Figure 167*; Eyde, 1967, *Figures 5–8*). Baumann (1946) found that the Araliaceae differ among themselves in this regard,[1] but his observations were not detailed enough for our purpose; so we surveyed the family to establish the taxonomic distribution of the differences. Simultaneously, and for like reasons, we examined our material for differences in the position and the degree of union of ventral bundles.

MATERIAL, METHOD

TABLE 1 lists the collections from which our observations are taken, together with the manner of preparation. Whenever possible, we used fluid-preserved specimens, usually flowers, occasionally fruits. Some we collected ourselves; others were obtained from helpful colleagues (*see* acknowledgments); for the most part, however, we had to make do with herbarium material, as indicated in the table. Herbarium specimens of most Araliaceae carry a great many flowers or fruits; so a few can usually be taken for anatomical study without detriment to the collection. In most cases, we removed two to four flowers for serial sectioning and

[1] Baumann (later known as Baumann-Bodenheim) had his own manner of describing the derived form of the gynoecial vascular system. Where we say the dorsal carpel bundles are united with peripherals, he would say the carpel bundles are absent (Baumann, 1946, p. 63 and *Table 1*).

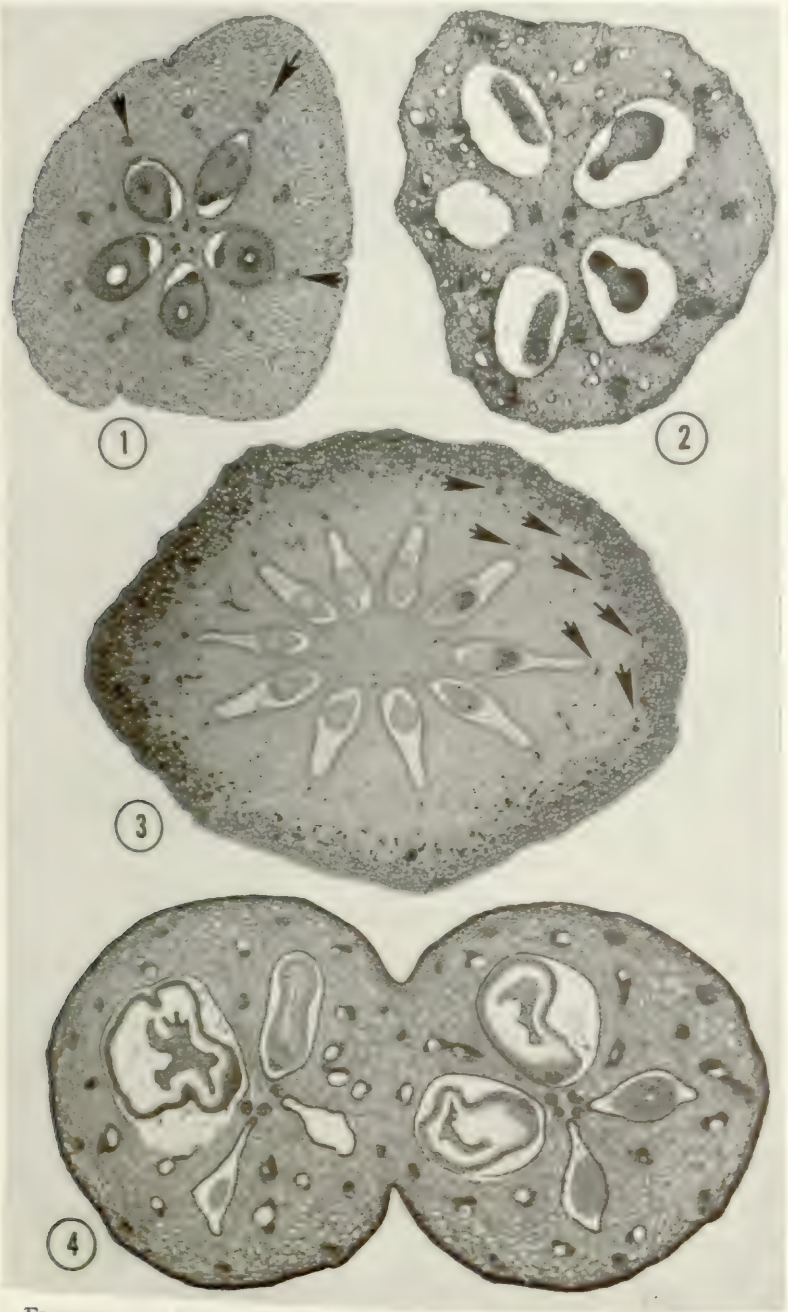
a similar number for clearing; however, we occasionally made our observations from a single flower, found nothing of much interest, and declined to remove others from the sheet.

We sectioned the flowers transversely, supplementing with longitudinal sections only in the case of *Tetraplasandra* (on which we have written a separate paper; Eyde & Tseng, 1969). We cleared whole flowers by treating them with NaOH and chloral hydrate, then passed them through an ethanol series into toluene for examination. If this treatment did not reveal the vascular system in sufficient detail, we next transferred the cleared flowers from toluene to melted paraffin, cast the paraffin into blocks, and cut the blocks into pieces with a razor blade, using a dissecting microscope to orient the smaller specimens. When we subsequently dissolved away the paraffin matrix with toluene, the cut pieces often showed vascular detail not visible in whole cleared flowers.

OBSERVATIONS

Tables 2 and 3 summarize the important features of gynoecial vasculature for each of the examined species; the tables also list the number of petals, stamens, and carpels for each. Sepals are not listed because the calyx is often poorly developed or lacking in Araliaceae. In Table 2, species are arranged in four groups, according to whether their flowers are best described as polymerous, 5-merous in all whorls, 5-merous with 2-merous gynoecium, or 5-merous with 1-locular gynoecium. Assignment is rather arbitrary in some cases, but most species fall readily into one or another of these groups. Literature citations accompany a few of the entries; in such cases, the vascular characters are not our own observations but are taken from an illustration or from descriptive comments in the cited work. *Tetraplasandra* species vary so greatly with respect to meristic characters that we decided to list them separately (Table 3).

In many species of Araliaceae — especially those with polymerous flowers — the number of floral appendages in each whorl varies from flower to flower. Obviously, we could not expect to establish the limits of variation for such species by examining only a few flowers of each (moreover, some of the flowers had petals or stamens missing); therefore, the counts given in Table 2 rely heavily on published descriptions. Several of our entries for petals and stamens of *Oreopanax* species are based on Smith's (1941) generic description in *North American Flora*, in which flowers are said to be "5 (rarely 4- or 6)-merous." In general, Smith's treatment does not give the numbers of floral parts for individual species. We use quotation marks wherever we have made no count of our own. For the most part, however, we did make one or more counts which fell within the limits given in the literature; in such cases we list the literature limits without quotation marks. When our count deviated from the counts of other authors, we usually expanded the literature limits to accommodate our observation. For instance, Clarke's treatment of *Schefflera* (*Heptapleurum*) *khasiana* in Hooker's *Flora of British India* (*see* generic de-



FIGURES 1–4. Transverse sections through inferior ovaries of Araliaceae. FIGURE 1. *Oreopanax nitidus*, *Cuatrecasas 27539*; dorsal carpel bundles (arrows)

scription, vol. 2, p. 727) would indicate that the flowers are completely 5–6-merous, but we count 9 ovary locules, so our entry in the GYNOECIUM column of TABLE 2 is 5–9 to accommodate Clarke's count as well as our own.

In two cases, however, we list only our own count, because we are not confident that the specimens are correctly identified. One of these is *Boerlagiodendron novo-guineense*: our preparation has 12 carpels, whereas Harms (1894, p. 31) lists this species among those with "Fruchtknotenfächer 7–9." The other is *Gastonia boridiana*, reportedly 8–10-carpellate (Harms, 1938a), but 15-carpellate in our preparation.

It is not always easy to characterize the degree of union between dorsals and peripherals. To be sure, there are taxa (*Peekeliopanax*, for instance) in which all dorsals are distinctly separate, even in sections taken near the base of the ovary; and there are others in which the dorsals are intimately united with peripherals up to the summit of the ovary. But there are also taxa in which the dorsals are united with peripherals in the lower part of the ovary and free from the peripherals in the upper part. To complicate matters further, the several dorsals within a single gynoecium may be free in varying degree.[2] At first we planned to use only two symbols, + for united and − for separate, in the DORSALS column of our tables, but we found we needed a third symbol (int) for the many taxa that are intermediate. Of course, the addition of a third category did not eliminate uncertainties attributable to poorly differentiated vascular bundles, to less than satisfactory preparations, or to omissions in the works of other authors. These uncertainties are indicated by question marks.

Characters of the ventral bundles are treated in two vertical columns, one expressing the degree of union of each pair of bundles, the other their position. In most species, the pairs are readily characterized as separate or united (if the separation is at the placental level only, a frequent condition, we consider the ventrals united), but an intermediate designation was necessary in certain cases. The ventral supply of a few species is anomalous. In *Meryta sinclairii*, for instance, it consists of a complex of slender anastomosing strands with no apparent symmetry. In *Tetraplasandra racemosa* the ventral system is seen in cross section as a series of vascular patches arranged in a circle, with most patches containing several discrete xylem strands. The ventral system of *Plerandra vitiensis* has a somewhat similar appearance, but only in the upper half of the

[2] This is true of our specimens of *Hedera helix*, for instance. Apparently, other authors have observed little or no union of dorsals and peripherals in this species (Eames & MacDaniels, 1947, p. 352; Philipson, 1967).

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united with peripheral bundles, duplex ventral bundles heterocarpellous (i.e., aligned with the septa, *see also* FIGURE 10); × 26. FIGURE 2. *Oreopanax* aff. *oerstedianus*; somewhat oblique section; ventral bundles fewer than carpels, appear to be homocarpellous; × 53. FIGURE 3. *Schefflera quinduensis*; dorsal bundles (inner arrows) and peripheral bundles (outer arrows) separate, ventral bundles anomalous (*see* text); × 20. FIGURE 4. *Hedera helix*; double ovary (*see also* FIGURE 8); ventrals on left are fewer than carpels; × 13.

TABLE 1. **Collections, Preparations**

SPECIES	COLLECTOR'S NAME & NUMBER [a]	LOCALITY	PREPARATION [b]
Acanthopanax giraldii Harms	*Purdom 445* (US)	Shensi	hfl, xs, cl
	Wilson 1971 (A)	Szechwan	hfl, xs
	Ching 887 (GH)	Szechwan	hfr, xs
Acanthopanax gracilistylus W. W. Sm.	*Ching 20481* (A)	Chekiang	hfl, xs
	Wilson 379a (US)	Hupeh	hfl, cl
	Steward, Chiao, & Cheo 258 (A)	Kweichow	hfr, xs
Acanthopanax henryi (Oliv.) Harms	*Henry 4832* (GH)	Hupeh	hfl, xs
	Wilson 1977 (A)	Hupeh	hfr, xs
Acanthopanax innovans (Sieb. & Zucc.) Franch. & Sav. = *Evodiopanax innovans* (Sieb. & Zucc.) Nakai	*Wilson 6998* (A)	Japan	hfl, xs
Acanthopanax koreanus Nakai	*Haio 2916* (A)	Korea	hfl, xs
Acanthopanax leucorrhizus (Oliv.) Harms	*Wilson 1967* (A)	Hupeh	hfl, xs
Acanthopanax senticosus (Rupr. & Maxim.) Harms	*Skvortzov s.n.* (A)	Manchuria	hfl, xs
Acanthopanax sessiliflorus (Rupr. & Maxim.) Seem.	*Smith 303* (A)	Hopeh	hfl, xs
Acanthopanax setchuenensis Harms ex Diels	*Wilson 1968* (A)	Hupeh	hfl, xs
	Giraldi s.n. (A)	Shensi	hfr, xs
Acanthopanax spinosus (L.f.) Miq.	*Suzuki "480003"* (A)	Japan	hfl, xs
	Muroi 3658 (A)	Japan	hfr, xs
Acanthopanax trifoliatus (L.) Merr.	*Handel-Mazzetti 796* (A)	Hunan	hfl, xs
	Henry 2253 (GH)	Hupeh	hfr, xs
Aralia elata (Miq.) Seem.	cult., U.S. Natl. Arbor.		pfl, xs, cl
Aralia spinosa L.	cult., U.S. Natl. Arbor.		pfl, xs, cl
Aralidium pinnatifidum Miq.	*Rahmat si Toroes 5440* (A)	Sumatra	hfl, xs

Arthrophyllum ahernianum Merr.	*Williams 1557* (GH)	Philippines	hfl, xs
	Ramos & Edano 44446 (A)	Philippines	hfl, xs
Arthrophyllum diversifolium Bl.	collector unknown (A)	Singapore	hfl, xs, cl
Astrotricha floccosa DC.	*Johnson & Constable 36621* (A)	Australia	hfl, cl
Boerlagiodendron novo-guineense (Scheff.) Harms	*Clemens 440* (A)	New Guinea	hfl, xs
Boerlagiodendron tetrandrum C. T. White	*Walker 260* (A)	Solomon Is.	hfl, xs
Brassaiopsis hispida Seem.	*Yü 20875* (A)	Yunnan	hfl, xs
Cheirodendron kauaiense Kraj.	*Hitchcock 15336* (US)	Hawaii	hfl, cl, xs
Cheirodendron trigynum (Gaud.) Heller	*Degener, Greenwell, & Murashige 20348* (US)	Hawaii	hfl, xs, cl
Cussonia paniculata Eckl. & Zeyh.	*Burchell 2400* (K)	South Africa	hfl, cl
Delarbrea lauterbachii Harms	cult., Bogor Bot. Gard. *XIII. J. 117*		pfl, xs
Delarbrea paradoxa Vieill.	*Lecard s.n.* (A)	New Caledonia	hfl, cl
Dendropanax chevalieri (Vig.) Merr.	*Norton 1363* (US)	Fukien	hfl, xs, cl
Dendropanax gonatopodus (Donn. Sm.) A. C. Sm.	*Pittier 16066* (US)	Costa Rica	hfl, xs, cl
Dendropanax querceti Donn. Sm.	*Standley 43039* (US)	Costa Rica	hfl, xs, cl
Didymopanax attenuatus (Sw.) March.	*Cooley 8337* (GH)	Windward Is.	hfl, cl
	Proctor 17992 (A)	Windward Is.	hfr, xs
Didymopanax morototoni (Aubl.) Decne. & Planch.	*Jiménez 3665* (US)	Dominican Rep.	hfl, xs, cl
	Gentle 2647 (A)	Brit. Honduras	hfl, xs
Diplopanax stachyanthus Hand.-Mazz.	*Tsang 22361* (A)	Kwangsi	hfl, xs
Dizygotheca elegantissima (Veitch) Vig. & Guill.	*Franc 2350* (A) (US)	New Caledonia	hfl, xs, cl
Eremopanax angustata Baill.	*Guillaumin, Baumann, & Hurlimann 15064* (A)	New Caledonia	hfl, xs
Fatsia japonica (Thunb.) Decne. & Planch.	*Takeuchi 402* (US)	Japan	hfl, xs, cl
Gamblea ciliata C. B. Clarke	*Kingdon-Ward 21093* (A)	Burma	hfl, xs
Gastonia boridiana Harms	*Brass & Versteegh 13139* (A)	New Guinea	hfl, xs

TABLE 1. **Collections, Preparations** (*continued*)

SPECIES	COLLECTOR'S NAME & NUMBER [a]	LOCALITY	PREPARATION [b]
Gastonia cutispongia Lam.	*Brown, Britton, & Wortley 1674* (NY)	Bermuda (cult.)	hfr, xs, cl
Gastonia papuana Miq.	Neth. Ind. For. Serv. bb 27220 (A)	South Moluccas	hfl, xs, cl
Harmsiopanax harmsii K. Schum.	*Hoogland & Schodde 7307* (US)	New Guinea	hfl, xs, cl
Hedera helix L.	cult., Arlington, Va.		pfl, xs, cl
Heteropanax chinensis (Dunn) Li	*Ching 8055* (A)	Kwangsi	hfl, xs
	Tsang 24584 (A)	Kwangsi	hfr, xs
Heteropanax fragrans (Roxb.) Seem.	*Wang 36212* (A)	Hainan	hfr, xs, cl
	Liang 63839 (A)	Hainan	hfl, xs
Indokingia crassa Hemsl.	*Fosberg 51970* (US)	Seychelles	pfl, xs; pfr, xs, cl
Kalopanax pictus (Thunb.) Nakai	*Wilson 1962* (US)	Szechuan	hfl, cl
Kissodendron australianum (F. Muell.) Seem.	*White 11717* (A)	Queensland	hfr, xs
Mackinlaya celebica (Harms) Philipson	*Clemens 7820* (A)	New Guinea	hfl, cl
Macropanax undulatus (Wall.) Seem.	*Yü 20163* (A)	Yunnan	hfl, xs
Megalopanax rex Ekm.	*Ekman 17551* (GH)	Cuba	hfl, xs
Merrilliopanax listeri (King) Li	*Tsai 54386* (A)	Yunnan	hfl, cl
Meryta sinclairii Seem.	*Walker 5391* (US)	New Zealand	hfl ♀, xs, cl
Myodocarpus involucratus Dubard & Vig.	*McKee 20484* (US)	New Caledonia	hfl, cl
Oplopanax horridus (J. E. Sm.) Miq.	*Cooper 28* (GH)	Michigan	hfl, xs
	Clemens s.n. (GH)	Montana	hfr, xs
	Anderson 935 (US)	Alaska	hfl, cl
Oreopanax floribundus (H.B.K.) Decne. & Planch.	*Cuatrecasas 27411* (US)	Colombia	pfl, xs, cl
Oreopanax nitidus Cuatr.	*Cuatrecasas 27424* (US)	Colombia	pfl, xs, cl
	Cuatrecasas 27539 (US)	Colombia	pfl, xs, cl

Oreopanax obtusifolius **L. Wms. = *O. guatemalensis*** (Lem.) Decne. & Planch.	cult., Bogor Bot. Gard. *XIII. J. 81*	pfl, xs
Oreopanax aff. *oerstedianus* March.	*Hladik 551*, Co	Panama pfl, xs, cl
Oreopanax sectifolius Cuatr.	*Cuatrecasas 27843* (US)	Colombia pfl, cl
Oreopanax xalapensis (H.B.K.) Decne. & Planch.		
Panax quinquefolius L.	*Stern, Eyde, & Ayensu 1981* (US)	Panama pfr, xs, cl
Panax trifolius **L.**	*Walker 1116* (US)	Virginia hfl, cl
Peekeliopanax spectabilis Harms	*Eyde s.n.*	Lebanon County, Pa. pfl, xs, cl
Pentapanax castanopsidicola Hayata	*Clemens 8641* (A)	New Guinea hfl, xs
Pentapanax subcordatus (Wall.) Seem.	*Wilson 10899* (A)	Taiwan hfl, xs
Plerandra insolita **A. C. Sm.**	*Forrest 26718* (A)	Yunnan hfl, xs
Plerandra solomonensis Philipson	*Greenwood 1048* (A)	Fiji hfl, xs
Plerandra vitiensis (Seem.) Baill.	*Brass 3320* (A)	Solomon Is. hfl, xs
	Greenwood 870 (A)	Fiji hfl, xs
	Degener 14380 (US)	Fiji hfl, cl
Polyscias grandifolia Volk.	*Moran 4566* (US)	Guam hfl, cl
Polyscias multijuga (A. Gray) Harms	*Smith 4837* (US)	Fiji hfl, cl
Polyscias nodosa (Bl.) Seem.	*Merrill 2484* (US)	Philippines hfl, xs, cl
Porospermum michieanum F. v. Muell.	cult., Brisbane Bot. Gard.	pfl, xs, cl
Pseudopanax arboreus (Murr.) Philipson	*Anderson 117* (US)	New Zealand hfl, cl
Pseudopanax crassifolius (Sol. ex A. Cunn.) C. Koch	cult., Strybing Arbor.	pfl, xs, cl
Pseudopanax davidii (Franch.) Harms	*Wang 66755* (A)	Yunnan hfl, cl
Reynoldsia pleiosperma A. Gray	*Vaupel 463* (US)	Samoa hfl, xs, cl
Reynoldsia sandwicensis A. Gray	*Hosaka 3651* (US)	Hawaii hfl, xs, cl
Schefflera bangii Harms	*Rusby 609* (GH)	Bolivia hfl, xs
Schefflera decaphylla (Seem.) Harms	*Ducke 1929* (A)	Brazil hfl, xs
Schefflera digitata J. R. & G. Forst.	*Walker 4954* (US)	New Zealand hfl, xs, cl
Schefflera khasiana (C.B.Cl.) Harms	*Yü 19477* (A)	Yunnan hfl, xs
Schefflera quinduensis (H.B.K.) Harms	*Daniel 3294* (US)	Colombia hfl, xs, cl

TABLE 1. Collections, Preparations (*continued*)

SPECIES	COLLECTOR'S NAME & NUMBER [a]	LOCALITY	PREPARATION [b]
Schefflera racemosa (Wight) Harms	*Theobald & Grupe 2369* (US)	Ceylon	pfr, cl
Schefflera robusta (A.C. Sm.) A. C. Sm.	*Smith P2291* (A)	Costa Rica	hfl, xs
Schefflera sciodaphyllum (Sw.) Harms	*Proctor 22250* (GH)	Jamaica	hfl, xs
Schefflera umbellata (N.E. Br.) Vig.	*Pinkus 153* (GH)	Venezuela	hfr, xs
Schefflera sp. ined.	*Hladik 330*, Co.	Panama	pfr, xs, cl
Sciadodendron excelsum Griseb.	*Allen 1604* (GH) (US)	Panama	hfl, xs, cl
Sinopanax formosanus (Hayata) Li	*Wilson 9734* (A)	Taiwan	hfl, xs
Stilbocarpa lyallii Armstr.	*Walker 4903* (US)	New Zealand	hfl, xs, cl
Stilbocarpa polaris (Hombron & Jacquinot) A. Gray	collector unknown (GH)	?	hfl, xs
Tetrapanax papyriferus (Hook.) K. Koch	*Steward, Chiao, & Cheo 740* (A)	Kweichow	hfr, xs
	Wilson 10895 (US)	Taiwan	hfl, cl
Tetraplasandra gymnocarpa (Hillebr.) Sherff	*Rock & Wilder 8827* (A)	Hawaii	hfl, xs
	Degener & Martinez 11920 (US)	Hawaii	hfl, xs, ls, cl
	Hopeman s.n. (US 690486)	Hawaii	hfl, cl
Tetraplasandra hawaiensis A. Gray	*Degener & Wiebke 2181* (A)	Hawaii	hfr, xs; hfl, cl
	Degener 24153 (US)	Hawaii	hfl, xs, ls
	Rock 10026 (US)	Hawaii	hfl, cl
	Hillebrand s.n. (US 809489)	Hawaii	hfr, cl
Tetraplasandra kaalae (Hillebr.) Harms	*Degener, Murashige, & Kerr 21018* (US)	Hawaii	hfl, xs, ls, cl
Tetraplasandra kavaiensis (H. Mann) Sherff	*Rock 12510* (US)	Hawaii	hfl, xs, ls, cl
Tetraplasandra lanaiensis Rock	*Rock 8088* (GH)	Hawaii	hfl, xs
	Munro s.n. (US 1091161)	Hawaii	hfl, cl
Tetraplasandra meiandra (Hillebr.) Harms	*Rock 8666* (A)	Hawaii	hfl, xs
	Degener 12988 (US)	Hawaii	hfl, xs, ls
	Degener, Lam, & Clay 19550 (US)	Hawaii	hfl, ls

	Degener & Desha 24159 (US)	Hawaii	hfl, cl
Tetraplasandra micrantha Sherff	*Hillebrand s.n.* (US 809378)	Hawaii	hfl, cl
Tetraplasandra paucidens Miq.	*Kanehira & Hatusima 13047* (A)	New Guinea	hfl, xs, cl
Tetraplasandra pupukeensis Skottsb.	*Degener, Murashige, & Kerr 21017* (US)	Hawaii	hfl, xs, ls, cl
Tetraplasandra racemosa Forbes = *Munroidendron racemosum* (Forbes) Sherff	*Stern, Carlquist, & Kato 1352* (US)	Hawaii	hfl, xs
Tetraplasandra waialealae Rock	*Rock 8870* (A) (US)	Hawaii	hfl, xs
Trevesia sp.	cult., U.S. Bot. Gard.		pfl, xs, cl
Tupidanthus calyptratus Hook. f. & Thoms.	cult., Univ. Calif. campus (Los Angeles)		pfl, cl; pfr, cl
	Henry 12298 (A)	Yunnan	hfl, xs, hfr, xs
	Henry 12298B (A)	Yunnan	hfl, cl
	Singapore Field No. 32568 (A)	Malaysia (West)	hfl, cl

[a] Herbarium designations for vouchers follow *Index Herbariorum*, except Co, which indicates a voucher still in the possession of the collector.
[b] hfl = herbarium flower, hfr = herbarium fruit, pfl = pickled flower, pfr = pickled fruit, xs = cross sections, ls = longitudinal sections, cl = cleared preparation.

ovary; at lower levels there are paired xylem patches in the septal radii, as in *Plerandra solomonensis*. *Schefflera quinduensis* shows an anomaly that we found nowhere else in the family: the ventral system is a double series (FIGURE 3), arranged so that each septal radius has two well defined vascular strands, one internal to the other. Another species of *Schefflera*, S. *khasiana*, also has supernumerary bundles in the center of its gynoecium, but they are not so symmetrically arranged with respect to the septa.

Ventral bundles can be united, or merely associated in pairs, in either of two ways: if the united bundles belong to adjacent carpels, the union is heterocarpellous; the union is homocarpellous if the united ventrals belong to the same carpel.[3] Since homocarpellous ventrals lie on the same radii as the dorsal bundles and heterocarpellous ventrals are on the septal radii (FIGURE 1), the two types of union are readily distinguished. Occasionally, however, one finds flowers in which the duplex ventral bundles are fewer than the carpels; the bundles may then be arranged asymmetrically with respect to the septa and to the dorsal bundles. This is the case in our material of *Hladik 551* (*Oreopanax* aff. *oerstedianus*, FIGURE 2) and we are therefore uncertain as to the original position of the ventrals, although they appear more homocarpellous than heterocarpellous. It is also true of *Reynoldsia sandwicensis*, and of some specimens of *Hedera helix* (FIGURE 4), but in these species the asymmetry does not obscure the true position of the ventrals. Our uncertainty concerning the position of the ventrals in *Harmsiopanax harmsii* and in *Cheirodendron kauaiense* is due to the difficulty of following weakly differentiated vascular bundles in sectioned herbarium flowers.

Baumann (1946) supposed homocarpellous ventrals to be the usual condition in araliaceous flowers (*see* his *Figure 3*, showing a "typical" gynoecium in cross section), even attributing this type of venation — quite wrongly — to *Schefflera* and to *Polyscias*. Actually, the heterocarpellous condition is far more common. We have found homocarpellous ventrals only in *Trevesia*, *Aralia*, *Panax*, *Stilbocarpa*, *Harmsiopanax*, *Mackinlaya*, and certain species of *Oreopanax* and *Acanthopanax*.

Miscellaneous observations on the lateral bundles of the carpels, on crystal complement, and on secretory structures are covered in the discussion section.

DISCUSSION, CONCLUSIONS

Polymery is primitive. — If our criteria for recognizing advancement are reliable, the question posed as our title is answered unequivocal-

[3] Hall (1954) coined these terms as "homocarpous" and "heterocarpous," but homocarpy, heterocarpy, and their adjectival derivatives have an older and more appropriate application (*see* van der Pijl, 1969, p. 82); hence the altered spelling. In his elaborate system for describing fruits, Baumann-Bodenheim (1955, p. 483) used "homocarpellate" and "heterocarpellate" to express symmetry and asymmetry of external form, but as far as we know no other author has followed his system; so our use of similar terms in a different sense should cause no confusion.

ly by the data in the tables. Ventral bundles retain their individuality only in certain species with polymerous flowers and nowhere else, even if we should count the intermediate (int) cases as having paired ventrals. Group A also has the largest proportion of taxa with discrete dorsal bundles: nine of the 11 Group A genera that we examined have one or more species with free dorsals. One of the two exceptions, *Boerlagiodendron*, is recognizably specialized by virtue of its sympetalous corollas. It is possible that the Group A genera missing from our survey (TABLE 4) contain a few additional species with advanced vascular characters. The insertion into Group A of additional taxa with derived vasculature would not alter our principal conclusion, however, that this group retains within it the primitive floral characters of the family.

Group B has relatively few species with discrete dorsal bundles, and these species belong to only four of the 15 genera listed. *Schefflera*, the only one of the four with species in both Group A and Group B, appears to be least advanced. Specialized characters found in the other three genera include capitate inflorescences (in *Oreopanax*), simple leaves (in *Dendropanax*), and prickly stems (in *Acanthopanax*).

No one doubts that 2-merous gynoecia are derived; therefore the preponderance of fused bundles in Group C serves to support our use of vascular characters as a guide to evolutionary advancement. This part of the table is not, however, without surprises. One unexpected finding is that *Tetrapanax*, with many specialized features, has markedly discrete dorsal bundles. It is less surprising to find discrete dorsals in the ovary wall of *Didymopanax*, for Frodin (ms) [4] merges *Didymopanax* with *Schefflera*, where discrete dorsals are not out of place. The relatively primitive vascular system of *Delarbrea*, together with its peculiar secretory structures and its geographic isolation on New Caledonia, place this genus (and its allies *Porospermum* and *Myodocarpus*) on an evolutionary line that diverged from other Araliaceae perhaps as long ago as the Cretaceous Period.

Comparison of species within certain genera provides additional evidence that our criteria are valid and that separate vascular bundles tend to occur in polymerous flowers. In *Plerandra*, the two typical species *P. vitiensis* and *P. solomonensis* have very primitive vasculature, as would be expected if polymerous flowers are primitive. The exception is *P. insolita*, which we assume to be a specialized member of the genus because of its highly modified inflorescence (*see* Smith & Stone, 1968, p. 477). In *Tetraplasandra*, the polymerous species *T. paucidens* and *T. hawaiensis* have the least specialized gynoecial vasculature; *T. racemosa*, the only other polymerous species examined, has an anomalous ventral supply, in keeping with its somewhat isolated position [5] within the genus.

[4] D. G. Frodin kindly allowed us to xerograph his impressive handwritten manuscript "The Complex of *Cephaloschefflera*" and to cite it here. The work is an interim report, written as part of Frodin's preparation for the doctorate in the Botany School of Cambridge University.

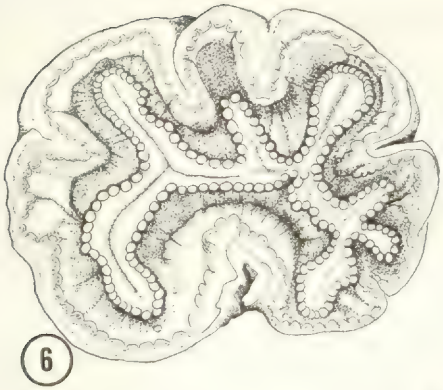
[5] As its name indicates, *Tetraplasandra racemosa* bears its flowers in racemes, rather than in umbels. Sherff (1952) considered it a separate monotypic genus.

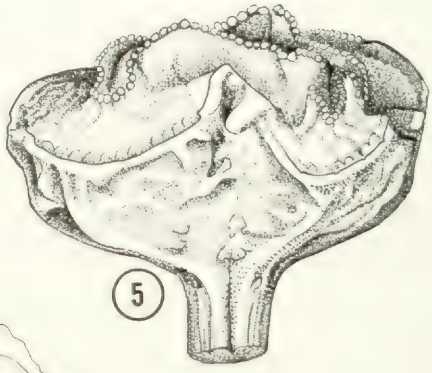
Meristic differences are similarly associated with vascular differences in *Reynoldsia*. The Hawaiian species *R. sandwicensis*, ecologically specialized and belonging to a derived flora, has fewer carpels than *R. pleiosperma* and other extra-Hawaiian species; it also has the more specialized vascular system of the two species we examined. Another genus with vascular characters that vary according to the species is *Schefflera*. Although *Schefflera* exhibits no simple relationship between meristic characters and the union of bundles (*see* our earlier comments on *Didymopanax*), neither does it contradict our conclusions. That is, the 5-merous examples in our study are not collectively more primitive than the polymerous examples.

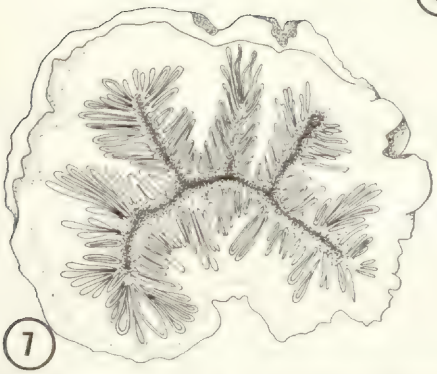
Although we believe the tables demonstrate beyond reasonable doubt the derivation of 5-merous flowers from polymerous flowers, we also recognize that at least a few Araliaceae have undergone a secondary increase in the number of floral parts. Certain species of *Plerandra* and *Tetraplasandra*, for instance, have a much greater number of stamens than their nearest allies, suggesting that evolution has progressed from "many" to "even more." The outstanding example, however, is *Tupidanthus calyptratus* (the only species of *Tupidanthus*). In this species, high polymery of the flower is associated with at least two specialized features: climbing habit and a calyptrate corolla so highly modified that no sutures distinguish its components. Furthermore, the flowers with the highest numbers of stamens and carpels tend to have a grotesque, fasciated appearance (FIGURES 5–7). Observing this, Delpino (1883, p. 215) and Rippa (1904) were reminded of the double flowers that occur occasionally in *Hedera helix* (FIGURES 4 and 8), and Rippa went so far as to propose that *Tupidanthus* is nothing but a *Plerandra* with double flowers.[6] This opinion was overlooked or ignored by Li (1942), who selected *T. calyptratus* as the most primitive living araliad.

Subdividing the family. — Our support of the long-entrenched concept of polymery as primitive in Araliaceae is not an endorsement of any of the several systematic treatments incorporating that concept. Indeed, we are convinced that no author has yet subdivided the family in a way that

[6] ". . . una *Plerandra*, i cui fiori sono normalmente e stabilmente divenuti dopii mediante la fusion di 2 fiori . . ." In support of this notion, Rippa figured a flower of *Tupidanthus* with one pedicel, two congenitally united ovaries, two androecial circles (side by side), and two sets of stigmas. We doubt that Rippa's explanation is completely correct, however. The word "fusion," and Rippa's use of the term "atavism" for his figured flower, seem to imply a gradual phyletic union, beginning with the close approximation of flowers and proceeding through intermediate stages in which the pedicels and then the ovaries are united. The fasciation of flowers in *Tupidanthus* is more likely caused by mutations that broaden the floral meristem. Such changes are known to play a major role in the fasciation of cultivated tomato fruits (Houghtaling, 1935; Luckwill, 1943; Zielinski, 1945). If this is true, Rippa's double flower is an extreme case of a derived condition rather than a throwback to an earlier condition. Furthermore, the supposed propinquity of *Tupidanthus* and *Plerandra* has been questioned: Frodin (ms) considers *Tupidanthus* more closely related to *Scheffleropsis subintegra* Craib (which is actually a *Schefflera*, Paratropia group, according to Frodin) than to any species of *Plerandra*.







FIGURES 5–7. A fruit of *Tupidanthus calyptratus, Henry 12298*, × 1.5. FIGURE 5. Viewed from side. FIGURE 6. Viewed from above. FIGURE 7. Cut transversely through upper part of locules, most of which are sterile. No attempt was made to represent all of the more than 200 stigmatic lobes and pyrenes.

shows evolutionary alliances. Harms (1894/1897), whose monograph is still the most complete — though it should not be used without also consulting his supplementary contributions covering the next 30 years — divided the Araliaceae into three principal groups. Earlier, Bentham and Hooker (1867) had recognized five main groups (as series), and Viguier (1906) later recognized 10 groups. Each of these treatments is artificial

FIGURE 8. *Hedera helix*; fruit developing from double ovary; × 7.5. A second example from the same plant is shown in transverse section as FIGURE 4.

to some extent, but the modification proposed by Hutchinson (1967a) is even more so.

Hutchinson's arrangement of the family follows that of Bentham and Hooker, except that he treats their series as tribes and adds two new tribes for species with solitary flowers in the inflorescences. The new tribes are placed first, in keeping with Hutchinson's view that non-umbelliferous inflorescences are in all cases more primitive than umbelliferous ones. Rigid adherence to this view obliges him to break up genera that are homogeneous except for inflorescence structure. Smith and Stone (1968) cite some of the weaknesses of Hutchinson's arrangement, pointing out the contradictions that arise in the genera *Polyscias* and *Plerandra*, among others, if characters of the inflorescence are overstressed, and Bernardi (1969) gives similar arguments against Hutchinson's treatment as it pertains to Madagascan araliads. Perhaps no genus confounds Hutchinson's emphasis on the inflorescence more effectively than *Meryta*, for the plants are dioecious, with staminate and carpellate inflorescences sometimes differing markedly. Hutchinson's key (1967a, p. 55), if applied to *M. sinclairii* and *M. choristantha*, would put carpellate plants in the tribe Cussonieae, staminate plants in the tribe Panaceae.

The floral characters customarily used to subdivide the Araliaceae yield groups that are only slightly more satisfactory than groups based on characters of the inflorescence. For instance, Viguier (1906) and Hutchinson (1967a) have placed together the genera in which some or all species have polyandrous flowers. In both arrangements, *Octotheca*, with three whorls of stamens, and *Dizygotheca*, with one whorl of stamens, are

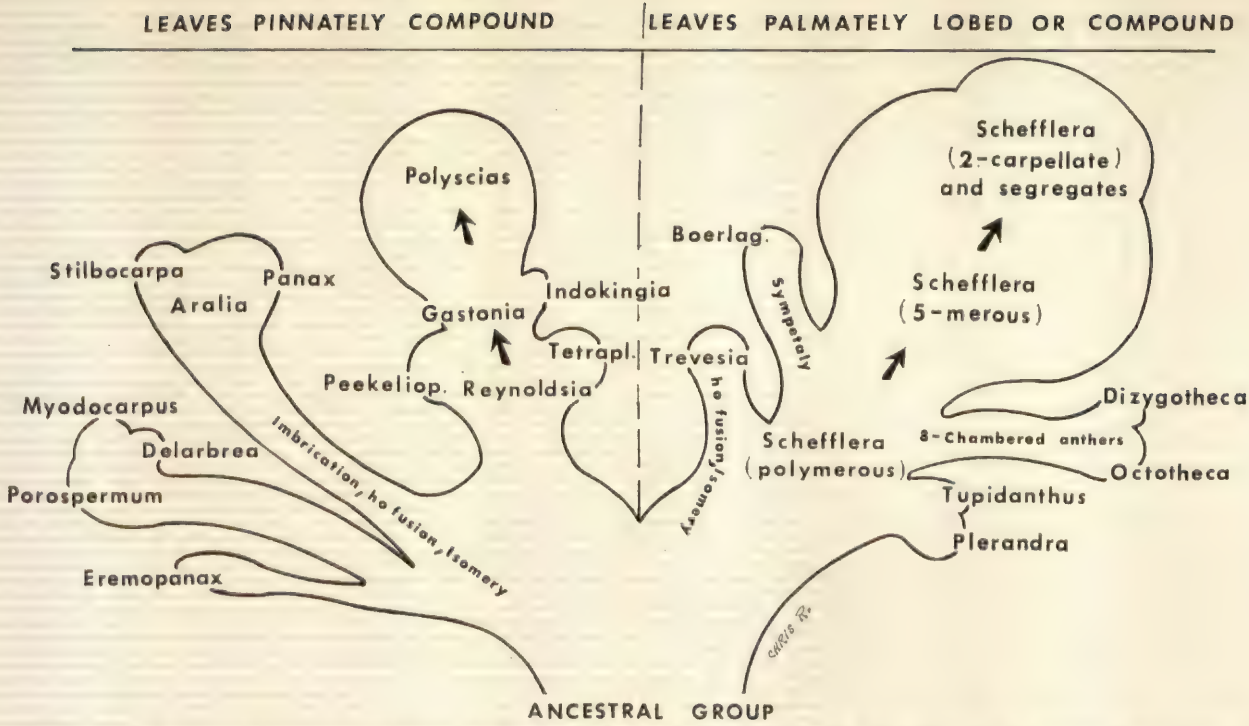


FIGURE 9. Suggested lineages within the Araliaceae. Most of the genera on the left side of the diagram have pinnately compound leaves; *Panax* and *Stilbocarpa* are exceptions. Those on the right have palmately lobed or palmately compound leaves (occasionally unifoliolate in *Schefflera*). Flowers of the ancestral group are thought to have been moderately polymerous, with a pair of ventral bundles for each carpel. Within the Araliaceae, imbrication of petals appears to be a derived condition. A principal feature of the diagram is that it divides the Plerandreae of earlier authors (*see* text).

assigned to different tribes. Yet these two genera are anatomically alike (Viguier, 1906, p. 136); they both occur in New Caledonia; and they share the 8-chambered condition of the anther found nowhere else in the family (Viguier, 1906, *Figures 26 & 41*).

Further evidence of the artificiality of a group based on polyandry alone is that it must include genera with pinnately compound leaves as well as genera with palmately compound or palmately lobed leaves. A more natural classification of the Araliaceae would result, we believe, if the primary division were to separate the palmate-leaved genera from the pinnate-leaved genera, and if this separation were continued wherever possible throughout the family. FIGURE 9 illustrates in a general way what we have in mind. The diagram includes only genera with primitive flowers plus a few others selected for their special interest. To include additional genera at this time would be unduly speculative; furthermore, we have no desire to duplicate the entanglements achieved by Harms (1894, p. 23) and by Viguier (1906, p. 176) when they attempted to link all genera of Araliaceae diagrammatically.

Our diagram breaks up the Plerandreae of Bentham and Hooker (1867) and of Viguier, making the component genera basal or near-basal in two main evolutionary lines. *Plerandra* and *Tupidanthus*, with palmately compound leaves, are near the base of an evolutionary line leading through the species of *Schefflera* with polymerous flowers to *Schefflera* species with 5-merous flowers and then to those with a 2-merous gynoecium. *Tetraplasandra*, with its close allies *Reynoldsia* and *Peekeliopanax*, is near the base of an evolutionary line leading through *Gastonia* to *Polyscias* and its derivatives, all with pinnately compound foliage. For various reasons, some of which are mentioned elsewhere in this paper, it seems likely that at least two lesser evolutionary lines share a common origin with the *Reynoldsia-Gastonia* line. One is a line leading to *Aralia*, *Panax*, and *Stilbocarpa*, the other a more ancient line leading to *Eremopanax* and the *Myodocarpus* group.

While arguing for greater emphasis on the form of the foliage — pinnate versus palmate — in subdividing the Araliaceae, we remain aware that certain exceptions must be made. *Panax*, with palmately compound leaves, and *Stilbocarpa*, with simple leaves, are closer to *Aralia*, with pinnately compound leaves, than they are to any genus in the *Schefflera* alliance. Also, the three genera of Harms's (1894) Mackinlayeae seem to form a natural group, by virtue of their clawed petals and their distribution, despite the fact that *Mackinlaya* usually has palmately compound leaves, *Pseudosciadium* has pinnately compound leaves, and *Apiopetalum* has simple leaves.[7] If these are the only exceptions, however, they do not greatly complicate a subdivision of the family in which the arrangement of leaflets is given primary importance.

[7] Simple leaves must be ignored in this discussion unless they are palmately lobed. It is clear that simple leaves with entire margins or dentate margins have evolved repeatedly in the Araliaceae, for they occur in very dissimilar species.

Position of ventral bundles and its significance. — From what is known of evolutionary trends in angiosperms, it is reasonable to assume that the syncarpous, inferior gynoecium of Araliaceae evolved from an apocarpous superior gynoecium, as we have indicated diagrammatically in FIGURE 10. Other changes shown in the figure are: reduction in the number of carpels, reduction in the number of ovules per carpel, homocarpellous union of ventral bundles, and heterocarpellous union of ventrals.

If ventral bundles were always positioned with diagrammatic symmetry and if the position, once established, could not change, taxonomists would have a superb tool for classification. Species with homocarpellous ventrals would perforce be assigned to a different evolutionary line from those with heterocarpellous ventrals. In reality, however, such a simple interpretation cannot be presented without qualification. One complication, already mentioned under OBSERVATIONS, is that the locules occasionally outnumber the ventral bundles; in such cases the designations "homocarpellous" and "heterocarpellous" may be difficult or impossible to apply. Another complication is that there are taxa in which the apparent position of the ventrals changes with the level of the cross section. In scanning a series of cross sections from *Hedera* or from *Fatsia*, for instance, one observes that the ventral bundles are heterocarpellous through the lower levels of the gynoecium but converge in the upper half of the gynoecium into a central plexus; just below the insertion of the ovules they become reestablished as discrete bundles in the homocarpellous position. Singh's (1954) drawings of transverse and longitudinal sections show these changes very nicely for *Hedera nepalensis*.

The diversity of ventral vasculature within *Oreopanax* and *Acanthopanax* is the most bothersome complication of all. *Oreopanax* has not been monographed. It appears to us to be an artificial genus, and this could account, at least in part, for its vascular heterogeneity. *Acanthopanax*, on the other hand, has had the attention of Harms (1918) and of Li (1942). We are satisfied that in this case the vascular variations occur within a group of related species. Among the Group B species of *Acanthopanax* that we have examined, *A. henryi* and *A. leucorrhizus* seem least aberrant: the ventral bundles are in the heterocarpellous position except for a narrow asymmetric-to-homocarpellous region in the vicinity of ovular insertion. In *A. senticosus*, the ventrals are heterocarpellous below the locules, homocarpellous near the ovules, and asymmetrically arranged at intermediate levels. The ventral supply of *A. setchuenensis* and *A. giraldii* can be either heterocarpellous or homocarpellous; that is, both patterns are found in the same species. In this respect, these two species differ from all others in our study.

The evolutionary causes for this variation in the ventral vascular supply probably involve genetic modification of the direction of vascular differentiation. Data on vascular differentiation in flowers are scanty. It is known, however, that the procambium develops acropetally and continuously in some carpels, including those of certain primitive angiosperms

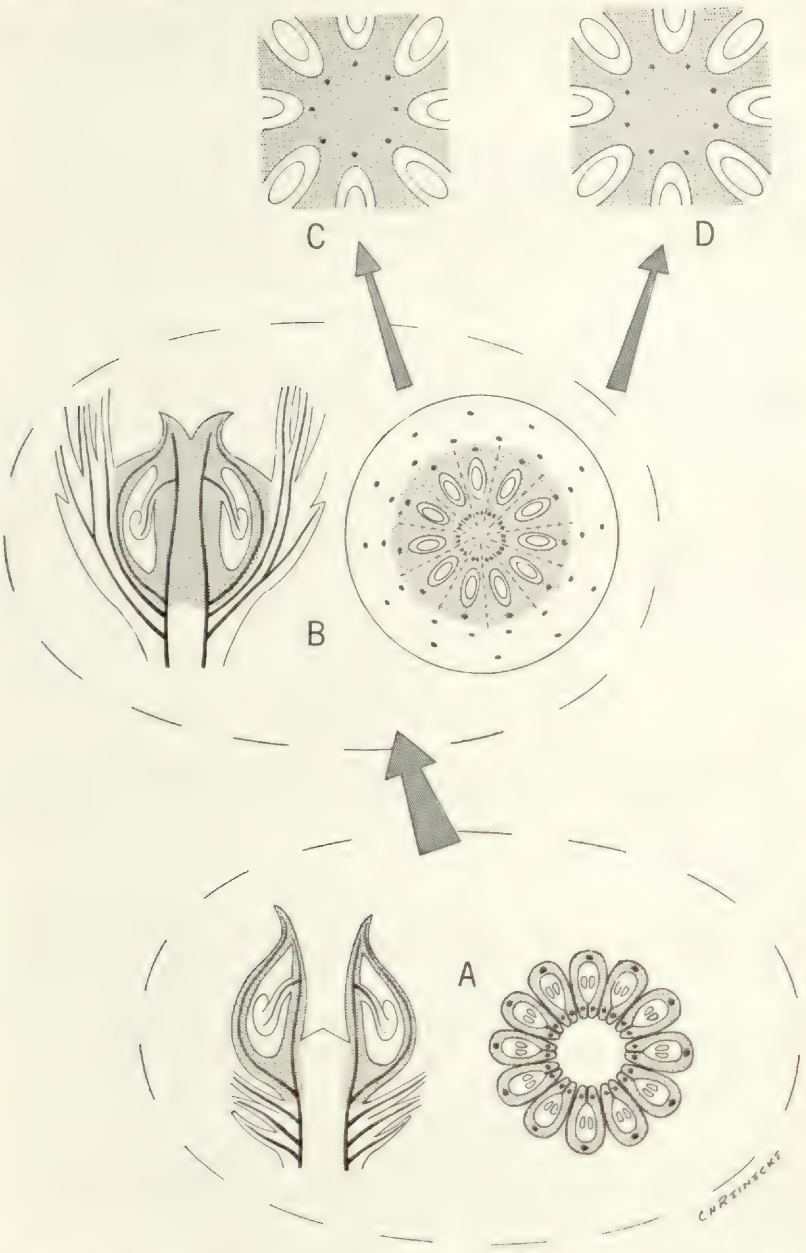


FIGURE 10. Origin of homocarpellous and heterocarpellous ventrals according to orthodox concepts of floral evolution. (A) Polymerous, apocarpous gynoecium with two ventral bundles and two or more ovules per carpel. (B) Later stage — primitive for Araliaceae — with united carpels, inferior ovary,

(Tucker, 1959, 1961; Tucker & Gifford, 1964). In the gynoecia of other species, however, procambial differentiation is basipetal or bidirectional, (summarized by Esau, 1954, and Tucker, 1959; *see also* Paterson, 1961). We conjecture that the ventral bundles of primitive Araliaceae developed acropetally and that subsequent genetic changes have introduced varying degrees of basipetal differentiation — from the ovule toward the receptacle — in certain taxa. Basipetally differentiating procambial strands would tend to be in the homocarpellous position because of the more or less median insertion of the single fertile ovule, and the junction of these homocarpellous strands with acropetally differentiating heterocarpellous strands would necessarily be a region of asymmetry or anastomosis. This conjecture is in keeping with our observation that the ventral bundles are always heterocarpellous in Araliaceae with polymerous flowers (*Trevesia* excepted), whereas the mixed or transitional condition occurs only in a few Group B taxa. The existence of these few transitional forms suggests the manner in which the homocarpellous pattern could have arisen here and there among the 2-carpellate (Group C) Araliaceae. Similar reasoning can be invoked to explain the diversity found in the Umbelliferae, in which the ventral bundles can be in either position (Jackson, 1933; Tseng, 1967), apparently without regard to major taxonomic groupings.

This is not to say that the hypothetical sequence in FIGURE 10 is completely incorrect or that the position of the ventrals has no taxonomic value. We suspect that the change from B to C illustrates fairly accurately the origin of the homocarpellous condition in *Trevesia*, because the flowers of this genus do not seem greatly advanced, and because one may find specimens in which the original paired condition of the ventrals is partially retained (Eyde, 1967, *Figure 11*). These pairs are always in the homocarpellous position, with no indication of secondary complexity; therefore, we have constructed FIGURE 9 so as to make *Trevesia* an early evolutionary offshoot of the *Schefflera* line. For like reasons FIGURE 9 shows the early divergence of a line leading to *Aralia*, *Stilbocarpa*, and *Panax* (perhaps *Harmsiopanax* belongs here too). Homocarpellous vasculature seems primary in this case — we have seen no exceptional or ambivalent specimens — and agrees with other features such as the form of the style and the estivation of the corolla in linking these genera together. Parenthetically, it should be added that differences in ventral vasculature may have value for distinguishing genera and species of Araliaceae even if the phylogenetic concepts expressed in FIGURE 10 should eventually prove false.

Additional characters. — While recording the vascular characters listed in TABLES 2 and 3, we scanned our serial sections for other features

single ovule per carpel; ventral bundles still in pairs. At still later stages, the paired ventrals unite as homocarpellous ventrals (C) or as heterocarpellous ventrals (D). This sequence explains the origin of some, but not all, ventral vascular systems in Araliaceae.

TABLE 2. **Gynoecial vasculature and meristic characters in selected Araliaceae**

Symbols in the DORSALS column show whether the dorsal bundles are predominantly separate from the peripheral bundles, −; united with the peripherals, +; or intermediate for this character, int. Similar symbols indicate the separation or union of paired ventrals, the ultimate form of union being a solitary central strand, ce. Pairing or union of ventrals may be homocarpellous, ho, or heterocarpellous, he; *see* FIGURE O. Other abbreviations identify anomalous vasculature, anom; asymmetry, asym; and items that are not applicable, NA. Further explained in text.

	DORSALS	VENTRALS UNION	VENTRALS POSITION	COROLLA	ANDROECIUM	GYNOECIUM
GROUP A, FLOWERS MORE OR LESS POLYMEROUS						
Tupidanthus calyptratus	−	+?	he	NA	many	up to 200+
Plerandra vitiensis	−	−	he	5	75-ca. 175	11–13
Plerandra insolita	+	+	he	"4–6"	"50–75"	9–12
Plerandra solomonensis	−	−	he	5	many	9
Peckeliopanax spectabilis	−	+?	he	6–12	25–66	6–22
Boerlagiodendron novo-guineense	+	int	he	11	11	12
Boerlagiodendron tetrandrum	+	−	he	4	4	8
Reynoldsia pleiosperma	−	+	he	10–11	10–11	20–22
Reynoldsia sandwicensis	+	+	he	8–12	8–12	7–12
Indokingia crassa	−	int	he	NA	up to 100	14–18
Gastonia boridiana	−	int	he	?	?	15
Gastonia papuana	−	int	he	5–9	7–55	6–12
Gastonia cutispongia	−?	+	he	"10–12"	"10–12"	9–12
Trevesia sp.	−	+	ho	7–12	7–12	7–12
Sciadodendron excelsum	+	+	he	9–10	9–12	9–12
Megalopanax rex	−	+	he	7–10	7–10	7–10
Schefflera quinduensis	−	+	he (anom)	8–9	8–9	8–10
Schefflera digitata	−	+	he	"5 or more"	"5 or more"	6–10 (or more?)
Schefflera khasiana	−	+	he (anom)	5–6	5–6	5–9
Schefflera racemosa	+	+	he	5–7	5–7	5–9
GROUP B, FLOWERS MORE OR LESS 5-MEROUS						
Schefflera decaphylla	−	+	he	5	5	5
Schefflera sciadophyllum	−	+	he	5	5	5
Schefflera bangii	+	+	he	5	5	5
Schefflera robusta	+	+	he	5	5	5
Schefflera sp. (*Hladik 330*)	+	+	he	5	5	5
Schefflera umbellata	+?	+	he	5	5	3–5
Oreopanax capitatus (Baumann-Bodenheim, 1955)	?	+	ho	4–6	4–6	5–10
Oreopanax obtusifolius	−	+	ho	4–6	4–6	5–7
Oreopanax xalapensis	+	+	he	4–6	4–6	4–6
Oreopanax nitidus	int	+	he	5	5	5
Oreopanax sectifolius	−	+	he?	5	5	5
Oreopanax aff. *oerstedianus*	−	+	ho? (asym)	5	5	5

TABLE 2. Gynoecial vasculature and meristic characters in selected Araliaceae (*continued*)

	Dorsals	Ventrals Union	Ventrals Position	Corolla	Androecium	Gynoecium
Oreopanax floribundus	int	+	he	5	5	4–5
Dendropanax chevalieri	–	+	he	5	5	5–6
Dendropanax querceti	–	+	he	5	5	4–5
Dendropanax gonatopodus	int	+	he	5	5	5–6
Aralia elata	+	+	ho	5–6	5–6	5–6
Aralia spinosa	+	+	ho	5	5	5
Dizygotheca elegantissima	+	+	he	5	5	5
Pentapanax castanopsidicola	+	+	he	5	5	5
Pentapanax subcordatus	+	+	he	5	5	5
Pseudopanax crassifolius	+	+	he	5	5	5
Fatsia japonica	int	+	he	5	5	5
Hedera helix	int	+	he	5	5	3–5
Hedera nepalensis (Singh, 1954)	+	+	he	5	5	5
Acanthopanax senticosus	–	+	asym	5	5	5
Acanthopanax leucorrhizus	int	+	he	5	5	5
Acanthopanax setchuenensis	+	int	he or ho	5	5	5
Acanthopanax henryi	int	+	he	5	5	3–5
Acanthopanax giraldii	–	+	he or ho	5	5	3–5
Gamblea ciliata	+	+	he	4–5	4–5	3–5
Cheirodendron kauaiense	+	+	he?	5	5	3–5
Cheirodendron trigynum	+	+	he	5–6	5–6	2–5
Meryta sinclairii	+	anom		4–6	4–6	3–6
Stilbocarpa polaris	+	+	ho	5	5	3–5
Polyscias nodosa	+	+	he	5	5	5
Kissodendron australianum	+	+	he	5	5	3–5
	GROUP C, GYNOECIUM 2-LOCULAR					
Polyscias multijuga	+	+	he	5–6	5–6	2
Polyscias grandifolia	+	+	he	5	5	2
Tieghemopanax elegans (Baumann, 1946)	+	+	he	5	5	2
Panax trifolius	+	+	ho	5	5	3
Panax quinquefolius	int	+	ho	5	5	2
Oplopanax horridus	int	+	he	5–6	5–6	2–3
Didymopanax attenuatus	–	+	he	5	5	2–3
Didymopanax morototoni	–	+	he	5	5	2
Brassaiopis hispida	int	+	ce	5	5	2
Macropanax undulatus	int	+	ce	5	5	2
Pseudopanax arboreus	int	+	he	5	5	2
Pseudopanax davidii	+	+	ce	5	5	2
Acanthopanax gracilistylus	–	+	he	5	5	2
Acanthopanax sessiliflorus	–	+	he	5	5	2
Acanthopanax koreanus	int	+	ce	5	5	2
Acanthopanax spinosus	int	+	he	5	5	2
Acanthopanax trifoliatus	int	+	he	5	5	2
Acanthopanax innovans	–	+	ho	5	5	2
Kalopanax pictus	+	+	he	5	5	2
Merrilliopanax listeri	int	+	he	5	5	2

TABLE 2. Gynoecial vasculature and meristic characters in selected Araliaceae (*continued*)

	Dorsals	Ventrals Union	Ventrals Position	Corolla	Androecium	Gynoecium
Cussonia paniculata	+	+	he	5	5	2
Heteropanax chinensis	+	+	he	5	5	2
Heteropanax fragrans	+	+	he	5	5	2
Astrotricha floccosa	+	+	he	5	5	2
Mackinlaya celebica	+	+	ho	5–6	5–6	2
Mackinlaya macrosciadea (Baumann-Bodenheim, 1955)	+	+	ho	5–6	5–6	2
Harmsiopanax harmsii	+	+	ho?	5	5	2
Harmsiopanax aculeatus (Philipson, 1970)	+	+	ho	5	5	2
Delarbrea lauterbachii	–	+	he	5	5	2
Delarbrea paradoxa	?	+	he	5	5	2
Myodocarpus involucratus	int	+	ho?	5	5	2
Porospermum michieanum	+	+	ho or ce	5	5	2
Stilbocarpa lyallii	+	+	ho	4–5	5	2
Tetrapanax papyriferus	–	+	he	4	4	2
GROUP D, GYNOECIUM 1-LOCULAR						
Diplopanax stachyanthus	–	+	NA	5	5–10	1
Arthrophyllum ahernianum	–	+	NA	5	5	1
Arthrophyllum diversifolium	–	+	NA	5	5	1
Eremopanax angustata	–	+	NA	5	5	1
Aralidium pinnatifidum	–	+	NA	5	5	1

TABLE 3. Gynoecial vasculature and meristic characters in Tetraplasandra

[Symbols and abbreviations as in TABLE 2]

	Dorsals	Ventrals Union	Ventrals Position	Corolla	Androecium	Gynoecium
T. paucidens	–	int	he	8–9	20–40+	9–11
T. hawaiensis	int	int	he	6–8	20–30	6–13
T. racemosa	+	anom		"5–6"	"10–20 (rarely 5)"	11–14
T. pupukeensis	int	+	he	6–10	ca. 20	5–7
T. waialealae	int	+	he	5–7	20–28	6
T. kavaiensis	+	+	he	6–9	6–9	2–5
T. kaalae	+	+	he	6	12–18	3–4
T. meiandra	+	+	he	5–8	5–8	2–5
T. lanaiensis	int	+	he	5–6	10–14	3
T. micrantha	+	+	he	8	7–8	2–4
T. gymnocarpa	NA	+	he	5–9	5–9	2–5

that would distinguish taxa or suggest evolutionary trends. We especially wanted to learn whether secretory canals, known to have taxonomic utility in the Umbelliferae, might aid in classifying the Araliaceae. Since many of our observations are based on herbarium flowers, with no con-

trol over developmental stages or quality of preservation, it would be pointless to attempt a description of secretory structures of each species, but a few generalizations can be made.

We found, for instance, that the number of secretory canals can differ greatly in gynoecia of different species, even closely related species. *Heteropanax fragrans* has an abundance of canals, whereas *H. chinensis* has few. Canals are abundant in flowers of *Acanthopanax senticosus*, rare in *A. giraldii* and *A. sessiliflorus*, confined to the vicinity of major vascular bundles in *A. koreanus*, and lacking in *A. leucorrhizus* and *A. setchuenensis*.

Secretory canals have a prominent place in the phylogenetic speculations of Baumann and Tikhomirov. Tikhomirov (1961) called the secretory structures of Araliaceae "rebernye kanal'tsy" (costal canals), indicating that they are found only in association with vascular bundles. If this were a reliable generalization it would tend to support his contention that *Hydrocotyle* and *Centella*, with closely associated canals and bundles, resemble Araliaceae more than they resemble apioid Umbelliferae.[8] We have found, however, that canals are associated with bundles in only a limited number of Araliaceae (examples occur in *Acanthopanax*, *Aralia*, *Oplopanax*, *Panax*, *Tetrapanax*). Baumann (1946) concluded from his studies that the ancestral Araliaceae were without secretory structures (*see* his summarizing table), but we see no evidence in support of this view. All of the polymerous flowers that we examined contained secretory canals, and the canals are scattered; that is, they have no noticeable tendency to accompany major vascular bundles. We failed to find secretory structures in the flowers of a very few species belonging to Groups C and D; viz., *Diplopanax stachyanthus*, certain species of *Acanthopanax*, *Aralidium pinnatifidum*, and *Stilbocarpa lyallii*.[9] *Aralidium* and *Stilbocarpa* would be considered advanced by any reasonable standards.

Our evidence indicates very emphatically that the gynoecia of ancestral Araliaceae were well supplied with scattered secretory canals, that the canals have been lost in a few of the derived taxa, and that they have been localized in others, including the Umbelliferae. In umbelliferous fruits the canals may be confined to ridges formed by major vascular bundles (Hydrocotyloideae) or to the grooves alternating with the ridges; some Umbelliferae have canals in both positions. Many older works call all of these canals vittae, whereas modern authors tend to use a separate

[8] Tikhomirov also claimed, as Håkansson (1952, p. 43) did, that the locules of Araliaceae lack the second, abortive ovule commonly found in locules of apioid Umbelliferae (but not in locules of *Hydrocotyle* and *Centella*). This is a puzzling error, for Harms's (1894, p. 8) monograph says abortive ovules (zurückgebliebende Samen) are not uncommon in Araliaceae, and other authors have confirmed the observation. Philipson (1970), who found vestigial ovules in all of the 30 or so genera of Araliaceae that he examined, suggests that the abortive structures take part in the transmission of pollen tubes (*see also* Håkansson, p. 34).

[9] Grushvitskiĭ et al. (1969) also found no secretory structures in *Stilbocarpa lyallii*, but attributed this to the poor quality of their material. We are somewhat uncertain about *Diplopanax*, for our observations were hindered by a darkly staining substance in the floral tissues.

term for canals that run with, and external to, the peripheral vascular bundles: extravasale Sekretkanäle (Baumann, 1946); ēkstrafastsikul-yarnye kanal'tsy, rebernye kanal'tsy (Tikhomirov & Galakhova, 1965); companion canals (Tseng, 1967). Companion canals develop somewhat differently from canals that do not accompany bundles (Kovács & Sárkány, 1968). This suggests that the two kinds of canals could contain different substances. It should be noted, however, that Lassányi & Lörincz (1970) report no histochemical differences between "pith canals" and "canals of the phloem" in stems of coriander.

Flowers of Araliaceae differ not only with regard to the distribution of secretory canals, but also with regard to the form and the distribution of calcium oxalate crystals. A survey of the family for crystals is beyond the scope of this article, but a few observations will serve to illustrate the diversity available for future taxonomic research. We found no crystals in the developing fruit wall of *Oplopanax horridus*, *Panax trifolius*, *Pseudopanax spectabilis*, or *Tetraplasandra gymnocarpa*; in contrast, scattered druses are abundant in the young fruit wall of *Boerlagiodendron novo-guineense*, *Plerandra vitiensis*, *Tetraplasandra hawaiensis*, *Trevesia* sp., and *Tupidanthus calyptratus*. The druses in *Tetrapanax papyrifera* are localized, mainly in the depressions that run longitudinally across the endocarp. Some of the araliads have two kinds of crystals, rhomboidal crystals in a narrow zone adjoining the endocarp tissue and druses scattered in the tissues external to this zone; examples are *Dizygotheca elegantissima*, *Plerandra solomonensis*, and *Tetraplasandra paucidens*. In *Delarbrea* and *Porospermum*, as in the related genus *Myodocarpus* (Baumann, 1946, *Figure 2*), druses are especially abundant in the ovarian septum. A similar concentration of druses occurs in the commissural region of certain Umbelliferae (Tseng, 1967, p. 39).

Our survey has not by any means exhausted the potential taxonomic utility of the gynoecial vascular system. Each carpel of an araliaceous gynoecium commonly has two or more conspicuous bundles in addition to the dorsal bundle and the ventral bundles. In some taxa, these intermediate or lateral carpel bundles are found in the septa between the locules (*Oreopanax obtusifolius*, *Trevesia* sp.; Eyde, 1967, *Figures 9 & 11*); in others they occupy a more peripheral position, where they may alternate symmetrically with the dorsal bundles (*Fatsia japonica* is an example; *see* Baumann, 1946, *Figure 24*). Intermediate bundles, like dorsal bundles, can be either separate from the peripheral bundles or united with them. In a few of the 2-carpellate taxa, the dorsal and the several intermediate bundles are arranged in a distinct circle around the endocarp tissue (*Delarbrea*, *Tetrapanax*). Some of the other 2-carpellate Araliaceae, such as *Astrotricha floccosa*, show the typical umbelliferous vascular pattern, in that there are 10 conspicuous bundles in the wall of the inferior ovary, each clearly representing the union of a carpel bundle with a peripheral bundle.

We do not wish to leave the subject of gynoecial vasculature without commenting on a feature that may prove useful in distinguishing the Um-

belliferae — at least the apioid Umbelliferae — from the Araliaceae. In both families, it is common for intermediate carpel bundles (lateral bundles of Umbelliferae) to turn inward through the upper part of the ovary and join the ventral bundles. The junction may take place at the level of ovular insertion (*Panax*) or very close to this level. In Araliaceae, the usual position of the junction is above the attachment of the ovule, but in the apioid Umbelliferae the junction is usually below the attachment of the ovule. The characteristic pattern for Araliaceae is shown in Philipson's (1967, p. 147) diagrams of *Hedera helix* and *Pseudopanax arboreus*; the pattern for Umbelliferae is exemplified by Jackson's (1933, p. 123) diagrams of *Osmorhiza longistylis*.

Ancestry and affinities of the Araliaceae-Umbelliferae complex. — Taxonomic opinion is divided as to the nearest allies of the Araliaceae and Umbelliferae.[10] Thorne (1968), Hutchinson (1967a, 1969), and Takhtajan (1969) adhere to the traditional concept of a close tie with Cornaceae. Others oppose this view (Eyde, 1967; Cronquist, 1968; Hegnauer, 1969; Philipson, 1970). We remain with the opposition, for our evidence indicates that the ancestral Araliaceae had, in addition to polymerous flowers, compound (probably pinnately compound) leaves and a normal ventral vascular system, features not found in *Cornus* or in any of the genera that can confidently be allied with *Cornus*.

According to Cronquist (1968, p. 278), the Araliaceae "would be perfectly at home in the Sapindales" — and close to Burseraceae — if the ovaries were superior instead of inferior. At his suggestion, we ran *Tetraplasandra gymnocarpa* through Hutchinson's (1967b) key to plant families: because of its hypogynous flowers, the species came out in Burseraceae as Cronquist predicted it would. Of course, the key could be adjusted quite easily to place *T. gymnocarpa* where it belongs, and we mention this point only to emphasize the similarity of certain Araliaceae to the Burseraceae. Secretory canals provide one link between the two families, pinnately compound leaves another. The ovules of Burseraceae are oriented in the same manner as those of the Araliaceae, but there are usually two fertile ovules per locule, a more primitive condition than that found in the Araliaceae. In other respects, the Burseraceae are more advanced. Vessel members of Burseraceae are always simply perforate (Metcalfe & Chalk, 1950), and none of the species have polymerous flowers. The seeds lack endosperm. Also, the ventral carpel bundles of the few burseraceous flowers that have been examined anatomically (Narayana, 1960a, 1960b) are united in the heterocarpellous position. From the mixture of primitive and advanced characters, it appears that neither family can be derived from the other. If the Araliaceae and the

[10] The Araliaceae and Umbelliferae have sometimes been linked with Pittosporaceae on anatomical grounds. Hegnauer (1969) and Jay (1969) recently revived this view, citing chemical similarities. The differences in floral structure separating Pittosporaceae from Araliaceae and Umbelliferae are so great, however, that we cannot envision a close common ancestry.

Burseraceae are allied, as the evidence indicates, both must have arisen from a common ancestral group. It then follows that the Araliaceae are also allied with the Rutaceae, for the affinity of Burseraceae to Rutaceae is well established. The addition of Rutaceae to the discussion makes Araliaceae seem even more "at home in the Sapindales" (Rutales of some authors), for a few of the Rutaceae have moderately polymerous flowers, and scalariform perforation plates have been observed in rutaceous woods (Solereder, 1908). The ventral bundles of Rutaceae with syncarpous gynoecia may be separate (*Coleonoma*) or united in either the homocarpellous (*Skimmia*) or the heterocarpellous position (*Ruta*; *see* illustrations in Gut, 1966).

The likelihood of a connection with Rutaceae recalls a suggestion put forward by Ehrlich and Raven (1967). Citing Dethier's (1941) finding that certain Rutaceae and certain Umbelliferae contain the same essential oils attractive to swallowtail butterflies, these authors suggested that the two families might share "a closer ancestral tie than had been suspected." Although a chemical link between Rutaceae and Umbelliferae seems to support our arguments, it also raises a question: Why have these essential oils not been found in Araliaceae? (At least one of them, methyl chavicol, occurs in Burseraceae; Roberts, 1923.) Of course, the answer may simply be that no systematic search for these compounds has yet been undertaken in the Araliaceae.

W. R. Philipson, whose recent work on Araliaceae has been directed toward delimiting troublesome genera, sent us one of his manuscripts (Philipson, 1970) as we were finishing our own. Independently, Philipson has made some of the same observations on gynoecial vasculature that we report. He also includes an interesting analysis of staminal vasculature which strengthens the case for the primitiveness of polymery in the Araliaceae. Our general conclusions are similar to his, with one main exception: Philipson suggests that the ancestral araliads had racemose inflorescences, and he mentions a number of taxa that he thinks may retain an indication of the original racemose condition. We believe at least some of Philipson's examples actually represent a secondary loss of umbels. For instance, Li's (1942) illustration of the spike-like inflorescence of *Diplopanax* shows most flowers in clusters of two and three, suggesting a previously umbellate condition. Moreover, there are associated characters in *Diplopanax* that also indicate advancement: the leaves are simple and entire, and the gynoecium is 1-locular. In *Cuphocarpus*, another of Philipson's examples (*see also* Hutchinson, 1967a, 1969), the partially racemose inflorescence is associated with 4-mery of the corolla and androecium, as well as a 1-locular gynoecium. Similarly, the racemose condition in *Pseudopanax* is associated with an advanced floral vascular system, heterophylly, and dicliny or polygamy. On the other hand, two of the genera that Philipson mentions, *Tetraplasandra* and *Schefflera*, exhibit independent indications of primitiveness; therefore we agree that the racemose or partially racemose inflorescences occurring in these genera may never have passed through an earlier umbellate stage.

We suspect, however, that some of the ancestral Araliaceae had more loosely branched inflorescences than the term "racemose" would indicate. The panicles of *Reynoldsia pleiosperma* and the more or less paniculate inflorescences of certain *Tetraplasandra* species suggest the manner in which various early Araliaceae may have borne their flowers.

Our conclusions concerning the ancestral characters of the Araliaceae agree well with current phytogeographic concepts in that the taxa we consider most primitive are all tropical. Moreover, many of them are found in southeast Asia and on islands of the western Pacific, that is, in the region believed to be "the cradle of the flowering plants" (Takhtajan, 1969; Smith, 1970).

SUMMARY

This investigation was undertaken in response to conflicting claims concerning the relative antiquity of polymery and 5-mery in Araliaceae. Assuming the degree of fusion of vascular bundles should be least in the least advanced flowers, we surveyed gynoecial vasculature throughout the family using standard clearing and sectioning methods. If the initial assumption is correct our findings show that 5-merous flowers are derived from polymerous flowers. Older taxonomic treatments err, however, in making *Tupidanthus* most primitive because of its highly polymerous flowers; in this genus, as in certain species of *Plerandra*, floral parts have increased. Furthermore, most treatments mistakenly place all polyandrous genera in the same subdivision of the family. We believe the polyandrous forms belong to two main evolutionary lines, one with pinnately compound leaves, the other with palmately lobed or palmately compound leaves. Position of ventral carpel bundles is of theoretical interest and may prove to be an aid to classification. In most Araliaceae the ventral bundles alternate with the locules. There are several taxa, however, in which the ventrals are aligned with the locules, and the genus *Acanthopanax* includes species that exhibit both patterns, apparently indicating the manner in which one type of ventral vascular system can be converted to the other. We judge that the ancestral Araliaceae had pinnately compound leaves, that at least some of the inflorescences were paniculate, and that the flowers were well supplied with secretory canals. We agree with others who have suggested an evolutionary link with Burseraceae and Rutaceae.

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TABLE 4. Genera not included in survey: meristic characters and comments

	COROLLA	ANDROECIUM	GYNOECIUM	
				GROUP A, FLOWERS MORE OR LESS POLYMEROUS
Plerandropsis	10	many	10	1 sp.; Tonkin. Separated from *Plerandra* by divided calyx lobes, palmately lobed leaves.
Octotheca	5	15	15–20	1 or 2 spp.; New Caledonia. Separated from *Dizygotheca* by 3 whorls of stamens.
Woodburnia	5	5	8–13	1 sp.; Upper Burma. Small prickly tree with palmately compound leaves, long calyx lobes, large flowers. Probably related to *Trevesia* (Harms, 1907).
Osmoxylon	8–10	8–10	8–10	2 spp.; New Guinea, Moluccas. Flowers sessile in heads.
Geepanax	8–10	8–10	5–10	1 sp.; Seychelles. Frodin (ms) unites this with *Schefflera* (Sciodaphyllum group).
				GROUP B, FLOWERS MORE OR LESS 5-MEROUS
Hederopsis	5	5	5	2 spp.; Malay Peninsula. 3-foliolate leaves; connate styles.
Bonnaya fatsia	5	5	5	2 spp.; Bonin Is. Related to *Fatsia*.
Apiopetalum	5	5	2–4	4 spp.; New Caledonia. Clawed petals, as in *Mackinlaya* and *Pseudosciadium*.
				GROUP C, GYNOECIUM 2-LOCULAR
Sciadopanax	5	5	2–3	3 spp.; Madagascar. Related to *Polyscias*.
Bonnetella	5	5	2	1 or 2 spp.; Society Is. Related to *Polyscias*.
Pulmeranda vidalii rockii	5	5	2	1 sp.; New Guinea. Intermediate between *Kissodendron* and *Polyscias*.
Motherwellia	5	5	2	1 sp.; Australia. Woody climber; 3-foliolate (sometimes only 1 leaflet). Linked to *Aralia* by imbricate petals.

Cephalaralia	5	5	2	1 sp.: Australia. Related to *Motherwellia* and *Aralia* (Harms, 1896, p. 22).
Seemannaralia	5	5	2	1 sp.: South Africa. 5-lobed palmate leaves. Segregated from *Cussonia*.
Pseudosciodaphyllum	5	5	2	1 sp.: New Caledonia. Pinnate leaves; unusual articulation of flower. Supposedly related to *Mackinlaya*, *Apiopetalum*.
Wardenia	5	5	2	1 sp.: Perak. Small armed tree with simple leaves. For cross section of fruit, *see* Philipson, 1970.
				GROUP D, GYNOECIUM 1-LOCULAR
Cuphocarpus	4	4	1	5 spp. (Bernardi, 1966): Madagascar. Pinnately compound leaves, unusual inflorescence (Hutchinson, 1969, p. 129). Related to and possibly derived from *Polyscias*.

terial from Harvard University while he was a Mercer Research Fellow at the Arnold Arboretum; courtesies extended by the directors and the curators of the Arboretum and of the Gray Herbarium are greatly appreciated. Drawings are by Anne V. Donovan (FIGURES 5, 6), Diane Robertson (FIGURES 7, 8), and C. H. Reinecke; photographs by Smithsonian photographers Andrew Wynn (FIGURE 3) and Victor Krantz. The National Science Foundation and the Smithsonian Research Foundation provided financial support through grants to Tseng (GB7988) and Eyde (SG625005) respectively.

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Note added in proof. While reading galley proofs for this article, we received two additional contributions by W. R. Philipson, "The Malesian species of *Gastonia*" (Blumea **18**: 490–495. 1970) and "A redefinition of *Gastonia* and related genera" (*Ibid.* 497–505). Philipson redefines *Gastonia* to include *Indokingia*, *Peekeliopanax*, and the extra-Hawaiian tetraplasandras. His findings make synonyms of certain entries in our tables: *Tetraplasandra paucidens* = *Gastonia papuana*, and *G. boridiana* = *Peekeliopanax spectabilis*, now *G. spectabilis* (Harms) Philipson. If *Tetraplasandra* is to include only Hawaiian species, it should occupy a slightly more advanced position than *Gastonia* in our FIGURE 9; otherwise our conclusions are not affected.

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SHOOT GROWTH AND HETEROPHYLLY IN ACER [1]

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IN *Acer* and many other woody genera, leaf form changes drastically and often abruptly during the life of the plant. Heterophylly is of two principal kinds in these woody plants: (1) changes during seedling and post-seedling stages, and (2) changes during the development of single annual shoots of adult plants. Type (1) is ubiquitous in *Acer*; type (2) is a regular feature of some species but uncommon or poorly expressed in others. These two types of heterophylly tend to converge; deviations in leaf shape on adult plants are often in the direction of seedling leaves. This tendency of woody plants to produce reversions, among other aspects of heterophylly, attracted a great deal of attention around the end of the 19th century, and much of our knowledge of these phenomena derives from that period. The principle that ontogeny tends to recapitulate phylogeny (Haeckel's biogenetic "law") was widely accepted by biologists at the time, and variations in leaf form during development offered many apparent illustrations.

Partly in reaction to such phylogenetic interpretations of variation in plant form, Goebel (1900) formulated the concept of heteroblastic development, which dealt with the same kinds of variations in ontogenetic and physiological terms. In plants exhibiting heteroblastic development, the juvenile and adult stages are markedly different, and the adult sometimes produces reversions to the juvenile state. Both features are illustrated by several common maples (Jackson, 1899). Their seedling leaves are either unlobed or slightly lobed, in contrast to the pronounced lobing of most adult leaves. In older plants, Jackson noted, a tendency toward reduced lobing reappears on sprouts and in leaves produced toward the tips of vigorous shoots; the latter is a regular feature of elongate shoots of *Acer pseudoplatanus* L. Schüepp (1929) established that these differences in leaf shape on a single shoot originate at an early stage of leaf ontogeny. His work is among the very few ontogenetic approaches to the neglected problem of heterophylly in woody plants.

The incidence of heterophylly in *Acer* and several other woody genera of temperate regions is closely associated with the specialization of the shoot system into long and short shoots. *Populus trichocarpa* (Critchfield, 1960) exemplifies this heterogeneous group, which includes *Ginkgo*

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biloba and representatives of *Betula*, *Cercidiphyllum*, *Liquidambar*, and *Parthenocissus* (Clausen & Kozlowski, 1965; Critchfield 1970a, 1970b; Smith, 1967; Titman & Wetmore, 1955). This link between heterophylly and shoot specialization is conspicuous in two maples of eastern North America: *Acer rubrum* L. (red maple) and *A. pensylvanicum* L. (striped maple). This paper describes shoot development in these species, surveys the patterns of shoot growth and incidence of heterophylly in other members of this genus, and compares *Acer* to other groups with similar patterns of shoot development and leaf variation.

MATERIALS AND TERMINOLOGY

The growth of leaves and internodes was measured at 4-day to 4-week intervals on long and short shoots of red and striped maples. Total leaf length was measured in 1957–58; in 1959 blades and petioles were measured separately. Observations of red maple were made on 5- to 10-year-old trees growing in natural stands on the Harvard Forest at Petersham, Massachusetts (1957, 1959) or in a plantation of Harvard Forest and other Massachusetts origins on the Case Estates of the Arnold Arboretum at Weston, Mass. (1958). Shoot growth of striped maple was measured in 1958–59 on young trees in two stands on the Harvard Forest. Sprouts were induced to develop by partial stripping of the buds and branches from small trees.

Other species of *Acer* were observed mostly in the Arnold Arboretum. Illustrated shoots and leaves are from Arboretum trees except *Acer orientale* L. (*A. creticum* L.), which I collected in the mountains of western Crete. Dried specimens were examined in the Gray Herbarium and the herbarium of the Arnold Arboretum.

Terminology follows that of an earlier paper (Critchfield, 1960). The *early leaves* expand when the buds open in the spring; the *late leaves* are produced subsequently. *Transitional leaves*, present on some annual shoots, are intermediate between early and late leaves in time of appearance, position on the shoot, and form. Leaves are numbered from the base of the annual shoot, and an internode has the same number as the leaf at its upper end. The *phyllochron* (Bond, 1945) is the time interval between corresponding developmental stages of successive leaves, excluding initiation (to which *plastochron* refers). The stage on which the phyllochrons are based here is leaf maturation, defined as 90 percent of final leaf or blade length. Blade length was preferred because of the great variation in growth duration and final length of petioles, particularly in red maple.

The term *epigenetic* is applied to the ontogeny of all leaves that are not preformed in winter buds. In contrast to the distinctly two-stage growth of preformed leaves, epigenetic development is continuous from initiation (or a very early stage of ontogeny) to maturation.

ORGANIZATION OF THE SHOOT SYSTEM

Acer pensylvanicum. — The long and short shoots produced by striped maple during a single season are distinct from each other in both stem length and leaf production. Short shoots greatly outnumber long shoots after the first few years of growth, and suppressed understory trees may not produce any long shoots. The short shoots almost invariably bear a single pair of the large leaves which typify this species, and terminate in a bud or inflorescence.

The stem of the short shoot rarely exceeds 5 cm. in length, and consists mostly of the internode below the single leaf-node. In a sample of 40 short shoots on herbarium specimens from widely scattered localities, the stems had a mean length of 2.0 cm. (range 0.3 to 4.6). An exceptional short shoot from Quebec had two similar pairs of leaves and a length of 2.0 cm., but all others had only one pair.

Long shoots of striped maple have more leaves (two or more pairs) and much longer stems than short shoots, and the length of the stem is roughly proportional to the number of leaf pairs. In a sample of 37 long shoots from six trees used for growth observations, 27 shoots had 2 to 4 leaf pairs and the others had 5 to 9. The stems ranged in length from 10.7 to 102.6 cm. Shoots with only two pairs of leaves averaged 18 cm. in stem length (range 10.7 to 28.4). The shortest long-shoot stem observed (on a herbarium specimen from Pennsylvania) had two leaf-nodes and was 7.4 cm. long. No shoots between 5.3 and 7.4 cm. were encountered.

Individual internodes are exceptionally long in this species. Many long shoots had at least one internode between 20 and 25 cm.; the longest observed was 28.5 cm.

Acer rubrum. — The annual shoots of red maple have smaller, more numerous leaves and shorter internodes than striped maple shoots. They terminate in vegetative buds; inflorescences are borne on separate non-leafy shoots in this species. As in striped maple, the long shoots are outnumbered by short shoots early in the life of the tree, and in the crowns of older trees they make up only 4 to 5 percent of the annual shoots (Wilson, 1966).

The long and short shoots produced in a single season are not as sharply distinct as in striped maple, but the great majority are readily classifiable as short (less than 2.5 cm.) or long (more than 3.0 cm.). Shoots with one or two pairs of leaves are nearly always short, and shoots with four or more pairs (ranging up to at least 16) are nearly always long. Shoots with three leaf pairs are extremely variable; those developing from terminal buds are usually short, but axillary buds sometimes produce long shoots with only three leaf-nodes. In a sample of 48 long shoots from six trees, the longest were 50 to 54 cm. and bore 12 to 16 pairs of leaves.

THE WINTER BUD AND ITS CONTENTS

Acer pensylvanicum. — The dormant vegetative buds of striped maple are remarkably uniform in construction and contents, and they offer no indications of the type of shoot they will produce the following spring. Nearly all have two pairs of bud scales, with only the outer pair exposed. As in other maples, the scales are modified leaf bases. The terminal buds are 6 to 10 mm. long; axillary buds are smaller (2 to 5 mm.), and some are rudimentary. In both this species and red maple, the envelope formed by the bud scales is much larger than the embryonic shoot it covers, leaving considerable space for the shoot to enlarge before the bud begins to expand.

With rare exceptions, the buds contain a single pair of embryonic leaves and a pair of primordia. In terminal buds collected at the end of the growing season, the embryonic leaves were 13 to 40 times as long as the primordia (TABLE 1). They were far advanced in development, having a short petiole and a blade with three nearly equal lobes and many teeth (FIGURE 1). The primordia were either undifferentiated in shape, as in FIGURE 1, or showed the beginnings of two lateral lobes. If a bud subsequently produces a short shoot, the embryonic leaves expand into the single pair of leaves on the shoot, and the primordia develop into the outer scales of the new winter bud. If the bud produces a long shoot, the primordia develop into the second pair of foliage leaves.

During bud expansion in the spring, the outer scales separate and the inner scales elongate. They form a loose envelope around the growing shoot, held tightly together along their margins by abundant tangled hairs. By the time they separate, both pairs of leaves have increased greatly in size (TABLE 1) and are densely pubescent. A new pair of primordia is initiated at the apex of most embryonic shoots during bud enlargement (TABLE 1).

The distinction between future long and short shoots was usually apparent during the later stages of bud enlargement. The primordia at the second node of future short shoots began to develop into bud scales. They grew at a relatively slow rate, and the leaf bases increased disproportionately in size. The first leaf pair was 16 to 38 times as long as the second in putative short-shoot buds. In this category were most axillary buds and the terminal buds of all short shoots and a few (3 of 20) long shoots. In buds that produce long shoots, the growth rate of the second pair of leaves was much faster, and by the time the buds opened pair 1 was only 3.3 to 16 times as long as pair 2. Most long-shoot terminal buds (17 of 20) and a few axillary buds were in this category.

A single terminal bud sampled at this stage (omitted from TABLE 1) differed from all others in having two pairs of well-developed embryonic leaves. The second pair was 40 percent as long as the first and 19 times as long as the pair of primordia at the apex. On the same tree, a bud like

TABLE 1. — **Bud contents and previous season's leaf production of Acer pensylvanicum and A. rubrum**

	A. PENSYLVANICUM			A. RUBRUM		
	Terminal buds			Terminal buds		
	Long shoots	Short shoots	Axil. buds	Long shoots	Short shoots	Axil. buds
BUDS DORMANT [1]						
No. of buds	15		5	9	14	1
No. leaf-nodes on previous season's shoot:						
Mean	4.1		–	7.8	2.0	–
Range	2–8		–	4–11	1–3	–
No. lf. pairs in bud:						
Mean	2		2	3	2.4	2
Range	–		–	–	2–3	–
Range in lf. length (mm.) at node:						
1	2.6–4.3		1.3–3.1	.80–1.2	.60–.90	.60
2	.05–.30		.02–.11	.50–.85	.25–.70	.30
3	–		–	.10–.35	.04–.20	–
BUDS SWELLING [2]						
No. of buds	20	3	41	33	20	14
No. leaf-nodes on previous season's shoot:						
Mean	4.0	1	–	7.9	2.0	–
Range	2–8	–	–	4–16	1–3	–
No. lf. pairs in bud:						
Mean	2.8	2.6	2.7	4.0	3.6	3.3
Range	2–3	2–3	2–3	3–5	3–4	2–4
Range in lf. length (mm.) at node:						
1	5.5–27	7.0–24	2.5–28	2.5–8.0	1.5–6.0	.60–5.7
2	.30–3.1	.40–1.0	.07–2.6	2.0–6.5	1.2–5.0	.37–3.5
3	.01–.15	.01–.10	.01–.15	.45–5.0	.15–2.2	.05–.70
4				.01–1.5	.01–.55	.01–.10
5				.01–.35	–	–

[1] *A. pensylvanicum* collected late Sept. and mid-Oct. from 2 trees. *A. rubrum* collected mid-Feb. from 1 tree.

[2] *A. pensylvanicum* collected mid- to late April from 4 trees; a few buds opening. *A. rubrum* collected same period from 6 trees.

this one apparently produced a single long shoot with two pairs of early leaves during the ensuing growing season (*see* next section).

Acer rubrum. — The dormant buds of red maple are much smaller (2.5 to 5.0 mm.) than those of striped maple, but they have more bud scales (6 to 12) and usually contain more leaves. The terminal buds of long shoots and some short shoots sampled in mid-winter had three pairs of leaves (TABLE 1), and the same number was reported by Wilson (1966). The other buds contained two leaf pairs. In buds with three pairs, pairs 2 and 3 were 67 and 22 percent as long as was pair 1 (ranges

60 to 78, 11 to 30). The embryonic leaves at nodes 1 and 2, despite their small size, had well developed, mostly glabrous blades with three nearly equal lobes and several marginal teeth, but only the largest had distinct petioles. The leaves at node 3 were unlobed if they were less than .15 to .20 mm. long, but above this size they had the beginnings of two lateral lobes.

In red maple, bud enlargement and the growth of the embryonic shoot was a gradual process that began long before the buds opened at the beginning of May. By mid-April, long-shoot terminal buds from the same tree sampled in February had nearly doubled in length, and the first pair of leaves had more than tripled (from 1.0 to 3.5 mm.). Pairs 2 and 3 had grown even faster, and were 79 and 37 percent as long as pair 1 (ranges 73 to 82, 28 to 42). Most red maple buds initiated an additional pair of primordia during enlargement (TABLE 1). A few

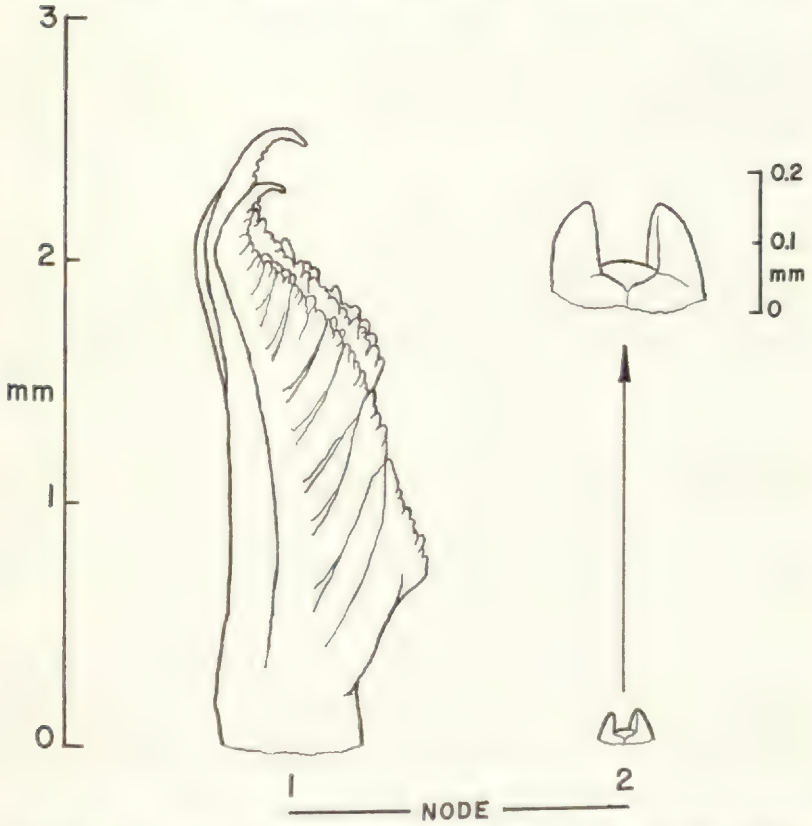

FIGURE 1. Contents of a winter bud of *A. pensylvanicum*. Collected in mid-October, this bud terminated a long shoot with seven pairs of leaves. One of the embryonic leaves at node 1 is omitted. The primordia at node 2 flank the dome-shaped apical meristem.

expanding terminal buds of long shoots (3 of 33) had five pairs of leaves (TABLE 1), but it is uncertain whether they had four pairs in the dormant bud or initiated two pairs during bud swelling.

Other species. — Expanding buds were collected in late April, a few days before bud opening, from a single tree of *Acer saccharum* Marsh. (sugar maple). This species lacks the specialized long and short shoots of red and striped maples. The buds were terminal or axillary on annual shoots 1.0 to 21.8 cm. long with 2 to 3 pairs of leaf scars. The nine buds in the sample had 8 to 10 pairs of scales and contained 3 to 6 pairs of leaves, the uppermost a pair of primordia. If the latter were initiated during bud expansion, as in red and striped maples, the dormant buds contained 2 to 5 pairs of leaves.

In *Acer platanoides* L., according to Moore (1909), the entire leaf complement of the next season's shoot is present in the winter bud. She found 3 to 4 pairs of leaves, the uppermost pair small and morphologically undifferentiated. Küster (1898) also reported three leaf pairs in the buds of this maple. The winter buds of another European species, *A. pseudoplatanus*, have 6 to 8 pairs of scales and 2 to 4 pairs of leaves (Schüepp, 1929).

GROWTH OF THE SHOOT

Red and striped maples are among the many temperate woody plants in which the principal shoots elongate until midsummer or later. Stem extension of red maple has been reported to continue until late June to late August in the northern U.S. (Kienholz, 1941; Jacobs, 1965).

Other maples belong to another large group of woody plants in which shoot elongation of plants past the juvenile stage is confined to a short period in the spring and early summer. *Acer saccharum* completes 90 to 100 percent of its stem extension in 17 to 35 days (Cook, 1941; Kienholz, 1941; Jacobs, 1965). It is widely assumed that shoot growth in this group, unlike the first, is restricted to leaves and internodes laid down in the bud. The evidence supporting this reasonable assumption is sparse, however, since few of the many investigations of stem extension in trees have paid much attention to bud contents or leaf production.

Acer pensylvanicum. — The inner bud scales separated at the end of April, when the buds were 2 to 5 cm. long, and were shed within a few weeks. The expansion of the embryonic leaves of the winter bud into the early leaves of the shoot was well under way by the time the bud opened.

The rapid growth of the early leaves continued through most of May. The blades reflexed and unfolded soon after emergence. The first pair of leaves on all measured shoots (14 shoots on 5 trees) reached 90 percent of their final length between May 28 and June 8 (FIGURE 2). A second pair of early leaves produced by a single long shoot matured 11.5

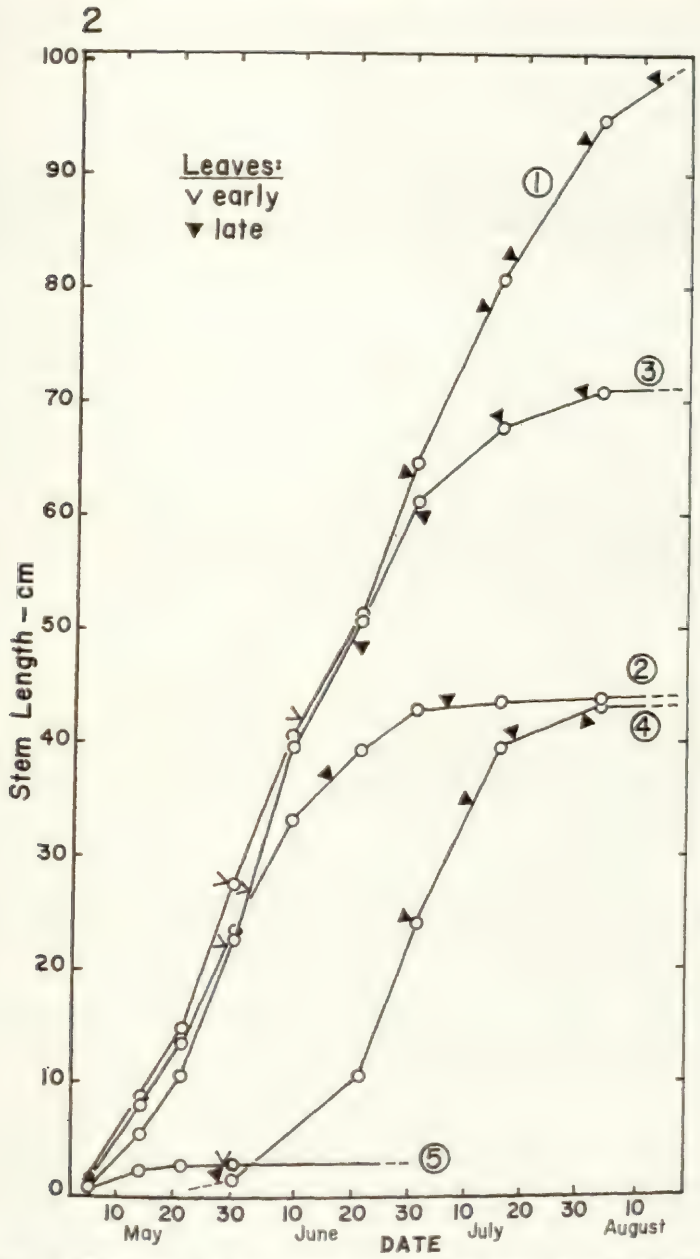

FIGURE 2. The timing of stem elongation and leaf maturation on *A. pensylvanicum* shoots. Triangles and V's indicate dates on which leaves reached 90 percent of their final length on three long shoots (1–3), one short shoot (5), and one sprout (4). Two additional pairs of leaves matured on shoot 1 before growth stopped.

days after the first pair (FIGURE 2: shoot 1). The petioles of the early leaves lagged behind the blades, reaching 90 percent of their final length an average of 11.1 days later (range 7 to 16).

The first internode, already 2 to 6 mm. long in elongating buds, grew rapidly after the shoot emerged. On both long and short shoots, it reached 90 percent of its final length in the latter half of May, 7.5 to 13 days before the pair of early leaves at its upper end. This internode elongated faster and reached much greater final lengths on long shoots: 5.2 to 14.5 cm. in the 37-shoot sample.

The expansion of the leaves at the first node, the extension of the stem below the node, and the development of a new winter bud completes the growth of non-flowering short shoots. The bud and the short internode separating it from the leaf-node developed slowly throughout the summer. The internode below the bud ultimately reached a length of 2.5 to 8 mm. The "stalked" bud, with its single pair of exposed scales, is a characteristic feature of the subdivision of *Acer* to which *A. pensylvanicum* belongs (section MACRANTHA PAX).

On long shoots, the first pair of late leaves began its most rapid growth in length in the third week of May, when the early leaves were about two-thirds of their final size. The phyllochron of the first late leaves was the longest on most shoots, averaging 18.3 days (range 16 to 21). Succeeding pairs of late leaves, all initiated during the growing season, developed at intervals of 14.1 days (range 4.5 to 20). The petioles matured after the blades, but the lag was shorter (mean 7.6 days) and more variable (range 0 to 21) than in early leaves.

The long internodes of the late leaves matured well before the corresponding leaves. They reached 90 percent of their final length 11.5 days earlier (range 6.5 to 17).

At the completion of extension growth, internode 2 was usually the longest on the shoot (FIGURE 12c). The only exceptions in the 37-shoot sample were three 2-node shoots, each with a longer basal internode, and three shoots with 5 to 9 leaf-nodes, on which internode 3 was the longest. One of the latter was the only shoot with two pairs of early leaves (FIGURE 2: shoot 1).

The final length of internodes decreased steadily from the longest internode to the shoot tip on long shoots with six or fewer leaf-nodes, but shoots with seven or more nodes had a second peak in internode length higher on the shoot, 3 to 5 internodes above the first. Most long shoots of *Populus trichocarpa* (Critchfield, 1960) and *Ginkgo biloba* (Critchfield, 1970a) also have two peaks in internode length, but the hormonal or other basis of this characteristic feature of long shoots is unknown.

Sprouts were produced by stripping branch systems of all vegetative buds in mid-April. The growth of one sprout was followed in detail (FIGURE 2: shoot 4). It appeared to originate from one of the rudimentary accessory buds which are sometimes present in the leaf axils of striped maple. The first small pair of leaves (FIGURE 6) matured in late May, when the sprout was only 1 cm. long; the second pair, much larger than

the first, did not reach 90 percent of their final length until more than a month later (FIGURE 2). By the time shoot growth stopped at the end of July, three more pairs of leaves had matured at intervals averaging 10 days (range 7.5 to 12.5). Leaf pairs 2 to 5 were like the late leaves of long shoots in all respects.

In a small defoliation experiment, the removal of the late leaves at an early stage of development drastically reduced the elongation of long-shoot stems. Three shoots on the same sprout clump were treated. Beginning in mid-May, leaf pairs 2 to 5 were cut off when they reached lengths of 1.2 to 3.0 cm. (FIGURE 3), and the cut surfaces were covered with lanolin. Stem extension, which is largely concentrated in internode 2 during late May and early June, continued almost normally for about 3 weeks. On two of the three shoots (FIGURE 3: B, C) the elongation of this internode was hardly affected by the treatment; its final length was 83 to 84 percent of the control. On the third treated shoot (A), the final length of internode 2 was only 38 percent of the control.

In early June, stem extension of all three treated shoots declined abruptly and permanently (FIGURE 3). Later-formed internodes were only 8 to 12 percent as long as corresponding internodes of the control shoot. Two shoots (B, C) began to die back from the tip in early July, after elongation had almost stopped. Shoot A subsequently produced a sixth pair of leaves, but by the end of the season all three treated shoots had died back to the first node.

Acer rubrum. — The buds opened in early May when they were 8 to 11 mm. long. The 2 to 3 pairs of early leaves on each shoot expanded rapidly through most of May. Early in development, the unfolding blade reflexed, forming an acute angle with the petiole.

The expansion of the first two leaf pairs was almost simultaneous. The phyllochron of pair 2 averaged only 1.0 days, ranging from −2.5 to + 4 days. (Negative phyllochrons were due to the maturation of pair 2 out of sequence.) If a third pair of early leaves was produced, it matured 2.5 to 5.5 days later, with a mean phyllochron of 3.4 days. All early leaves on a total of 17 shoots measured in three seasons reached 90 percent of their final length between May 25 and June 13. The petioles of the early leaves matured a mean of 10.1 days after the blades, and their variation in final length was reflected in the range of this interval: 5 to 20 days.

The internodes of the early leaves matured a week or more before the corresponding leaves. This interval could not be accurately estimated on short shoots, which rarely produce internodes more than 1 cm. long, but the longer internodes of early leaves on long shoots reached 90 percent of their final length 8.5 days before the leaves (range 5 to 13).

The growth of most short shoots of red maple was almost completed by early June (FIGURE 4: shoots 3, 6; FIGURE 9). Some short shoots later produced a pair of small transitional or late leaves, but their expansion was not accompanied by appreciable stem elongation. The new

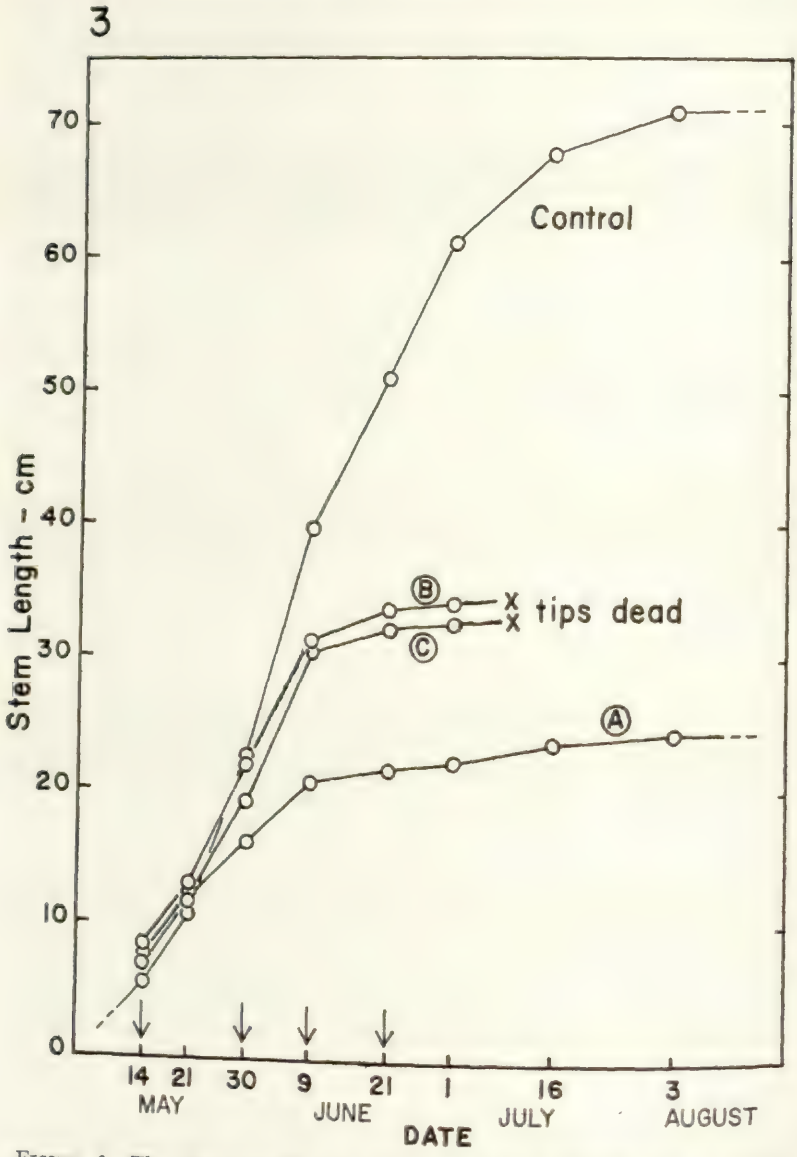

FIGURE 3. The effect of late-leaf removal on stem extension in *A. pensylvanicum*. A pair of developing late leaves was removed from each treated shoot (A–C) on dates indicated by arrows. Control is shoot 3 of FIGURE 2.

terminal buds of the short shoots developed slowly, reaching their final size in August.

The production of a second set of leaves on long shoots began after

a distinct hiatus in the continuity of leaf production. At this stage the early leaves and their internodes had nearly completed their growth, but the first pair of late leaves was only a fraction of its final size and its internode was still elongating (FIGURE 8). On the long shoots measured in 1957–58, the phyllochron of total length for the first pair of late leaves averaged 12.9 days (range 7.5 to 19); in 1959 the phyllochron of blade length for this pair averaged 8.8 days (FIGURE 4). On all shoots, this interval was 5 to 16 days longer than the preceding phyllochron and 1 to 9 days longer than the next.

Successive pairs of late leaves matured at intervals averaging 6.9 days (range 2 to 16). Their petioles tended to be relatively shorter than those of early leaves, and the interval between blade and petiole maturation was slightly less (mean 8.2 days, range 2 to 16).

The interval between internode and leaf maturation was also somewhat shortened on the late-leaf part of the shoot, and tended to decrease toward the shoot tip. Internodes matured an average of 5.7 days before the corresponding late leaves (range 0 to 12).

In their early stages the blades of late leaves are red-pigmented and strongly reflexed. This gives the crowns of actively growing red maples a characteristic appearance in early summer, when late-leaf production is at its height. Each of the principal branch systems, comprising a perennial long shoot covered with short shoots of various ages, terminates in a distinct reddish cone of developing late leaves.

When stem extension is completed, the internode separating the early and late leaves is usually the longest on the shoot. Most shoots from terminal buds have three pairs of early leaves, and internode 4 is usually the longest. On long shoots maturing from axillary buds, which more commonly have only two early-leaf nodes, internode 3 is usually the longest. In the 48-shoot sample, internode 4 was longest on 23 of 32 shoots from terminal buds, and internode 3 was longest on 12 of 16 shoots from axillary buds. Most of the exceptions were shoots with two peaks of internode length, on which internode 3 or 4 was the first peak and the second peak was the longest internode on the shoot.

As in striped maple, the incidence of two peaks in the final length of internodes along the shoot depends partly on number of internodes. In red maple it also varies from tree to tree, with two-peaked shoots uncommon or absent on some trees. In the 48-shoot sample, few (3 of 29) shoots with 4 to 8 internodes had two peaks, but 9 of 17 shoots with more than 8 internodes had two peaks 2 to 5 internodes apart (mean 3.5).

Other species. — The timing of leaf expansion was measured on five shoots of a single sugar maple growing at the Harvard Forest. The shoots developed from terminal buds of shoots that had produced 2 to 5 pairs of leaves the previous year. The buds opened in late April, and 2 to 4 pairs of leaves reached 90 percent of their final length during the last half of May at mean phyllochrons of 1.0, 1.2, and 5.8 days. One

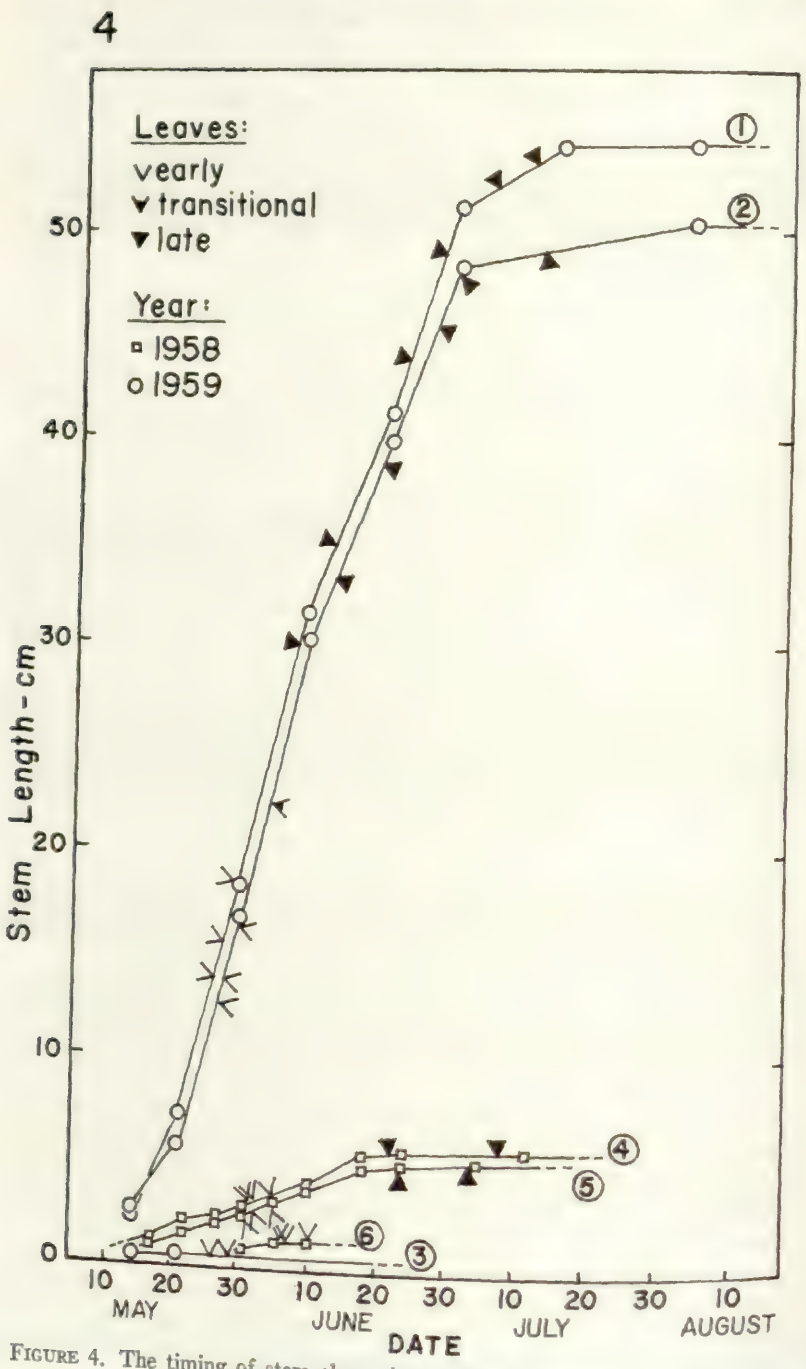

FIGURE 4. The timing of stem elongation and leaf maturation on *A. rubrum*

shoot produced a fifth and smaller pair of leaves which matured about 2 weeks after pair 4.

The development of a single heterophyllous long shoot of *A. pseudoplatanus* was described in detail by Schüepp (1929). The rapid expansion of the first three pairs of leaves after the bud opened was followed by a long pause before the second set of leaves began to mature. Phyllochrons of blade length (estimated from Schüepp's *Figure 4*) were 1 and 3.5 days for pairs 2 and 3, but pair 4 (the first late leaves, in the terminology used here) did not mature until 20.5 days later. Blades of the next six pairs of leaves matured at intervals of 7 to 12.5 days (mean 8.7). The petioles of all leaves matured 14 to 27 days after the blades. Stem elongation was continuous, and by the time it ceased in early August the shoot had 14 pairs of leaves. Its development differed from that of a comparable red maple shoot primarily in the longer interval between blade and petiole maturation, and the much longer phyllochron separating the early and late leaves.

VARIATION IN LEAF FORM

The early leaves of red and striped maples, developing from embryonic leaves in the winter bud, predominate in the crowns of all but the youngest trees. From the data of Wilson (1966) on red maple, it is estimated that they make up about 83 percent of the photosynthetic area of the crown of 5-year-old trees, and this proportion increases to 97 percent in trees 60 years old or more. The early leaves are usually the only leaves associated with the reproductive structures of maples. These are the leaves that have been utilized in the classification of the maples, since most plant collections sample parts of the shoot system bearing flowers and fruits. In taxonomic descriptions the early leaves are sometimes referred to as "typical," "ordinary," or "adult" leaves.

Leaves that are not preformed in buds are produced throughout the life of red and striped maple trees, although their relative number diminishes with age. In this category are such diverse types as the small leaves of first-year seedlings, the large leaves of vigorous sprouts, and the late leaves of long shoots. Also included are leaves of the lammas and disguised lammas shoots[2] regularly produced by young trees of *Acer platanoides*, *A. pseudoplatanus*, and other maples (Späth, 1912; Burger,

[2] Lammas shoots originate from partly developed buds during the summer, after the spring flush of growth is completed. Disguised lammas shoots ("Verkappter Johannistriebe": Späth, 1912) of maples differ in that the leaves whose enlarged bases function as bud scales also have expanded blades. These two intergrading shoot types may be most common in species that do not routinely produce long and short shoots; I have not encountered them in red or striped maple.

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shoots. Triangles and V's indicate dates on which leaves (1958) or blades (1959) reached 90 percent of final length. Shoots 3 and 6 are short shoots, the others long shoots. Three additional pairs of leaves on shoots 1 and 2 were too badly damaged by insects for growth measurements.

1926). All of these kinds of leaves develop epigenetically, and this common mode of ontogeny appears to be responsible for the tendency of leaves on these otherwise dissimilar kinds of shoots to resemble each other in shape.

In species with lobed leaves, including red and striped maples and many others, the lateral lobes of epigenetic leaves tend to be displaced downward on the blade, to project outward from the midrib at a greater angle, and often to be reduced in size. These leaves, borne mostly on "sterile" shoots, are poorly represented in herbaria. In taxonomic accounts they are sometimes referred to as "atypical," "extraordinary," or "juvenile" leaves.

Acer pensylvanicum. — The early leaves of striped maple are among the largest in the genus. They are bigger than any of the late leaves on the same shoot, but the two kinds of leaves overlap in size on different shoots. In a sample of both shoot types, the blade area of early leaves was 87–388 cm.^{2}; that of late leaves 14–179 cm.^{2} On the most vigorous long shoots (5 to 9 leaf-nodes) the biggest late leaves were 46 to 64 percent as large as the early leaves, but on long shoots with only two nodes the late leaves were much smaller (9 to 35 percent).

The two kinds of leaves also differ in shape. The more uniform early leaves terminate in three nearly equal lobes (FIGURE 5). The principal lateral lobes of the late leaves are shorter than the middle lobe and displaced basally (FIGURE 12a, e). The veins forming the axes of the lateral lobes were 79 to 98 percent as long as the midrib in the early leaves of the sampled shoots, 49 to 76 percent in the late leaves. The middle lobe of early leaves was 35 to 45 percent of the blade length; that of late leaves was 49 to 62 percent.

The lateral lobes are most conspicuously reduced at the first late-leaf node (FIGURE 5), and sometimes are no larger than the marginal teeth. Succeeding pairs of late leaves nearly always have reduced but definable lobes. The first pair of late leaves also tends to be narrower than the others, with relatively shorter petioles.

The first leaves of sprouts are small, unlobed, and coarsely toothed, but above the first node the leaves are indistinguishable from late leaves of long shoots in size and shape (FIGURE 6). This sequence in leaf shape is also followed on elongate sylleptic shoots — branches that develop directly from axillary meristems during the same season as the parent axis (Späth, 1912).

The first, and often the only, pair of leaves on first-year seedlings of striped maple are serrate but not lobed. Their similarity in shape to the unlobed leaves of older trees was pointed out by Deane (1896). They are much smaller, however, a few measured seedling leaves having blade areas of only 2.6–6.7 cm.^{2}

Acer rubrum. — Although red maple has an extensive infraspecific nomenclature based primarily on its variability in leaf shape, the differences

FIGURE 5. A developing long shoot of *A. pensylvanicum*. Collected at the Harvard Forest in early June, this shoot has one pair of nearly mature early leaves and two unfolded pairs of late leaves.

FIGURE 6. Mature leaves of a sprout of *A. pensylvanicum* (1 leaf per node). Except for leaf at node 1 (lower left), they are indistinguishable from late leaves of long shoots. Growth of this sprout is shown in FIGURE 2 (shoot 4).

between early and late leaves of the same shoot are not as pronounced as in striped maple, and transitions are common. The early leaves, like those of striped maple, generally have larger blades (Wilson, 1966).

Differences in leaf shape also parallel those of striped maple (FIGURE 12a, e). Early-leaf blades have three subequal lobes (FIGURES 8–10), in contrast to the elongate median lobe of late leaves (FIGURE 10). In a sample of long shoots, the midlobe was 46 to 56 percent of the blade length in early leaves, 60 to 70 percent in late leaves. The main lateral veins of the first two pairs of early leaves were 82 to 91 percent as long as the blade, but the third pair, which often has narrower blades (FIGURES 8, 10), sometimes fell within the range of the late leaves (65 to 79 percent).

The basally displaced and shortened lateral lobes of the late leaves tend to project outward from the midrib. The angle formed by their axes was 95–117°, compared to 73–86° in early leaves. This feature provided a consistent distinction between the two kinds of leaves in this species but not in striped maple.

The relative length of petioles tends to decrease from node to node, stabilizing somewhat in the late-leaf series (FIGURES 10, 12b). The petioles of early leaves were 60 to 114 percent as long as the blades; late-leaf petioles were 30 to 80 percent. As Wilson (1966) has pointed out, variations along the shoot in petiole length, together with changes in blade size and internode length, tend to minimize the mutual shading of leaves.

The leaves of red maple sprouts and sylleptic shoots resemble the late leaves of long shoots in their elongate median lobes, shortened and projecting lateral lobes, and short petioles (Jackson, 1899: pp. 99, 100, *Figure 27*). These tendencies reach their extreme expression in the leaves of first-year seedlings. The lateral lobes of seedling leaves are usually much smaller than the elongate median lobe (FIGURE 7; Jackson's *Figure 28*), and are sometimes reduced to teeth (Brayshaw, 1959: *photo.* on p. 28).

Other species. — This survey was largely restricted to maples with medium-sized or small leaves. Herbarium specimens of species with large simple leaves (e.g. *A. macrophyllum* Pursh) or compound leaves (sections TRIFOLIATA Pax and NEGUNDO (Boehm.) Maxim.) usually include only short stem segments and are not suitable for observations of shoot organization. The available specimens of first-year seedlings were supplemented by published accounts (Brayshaw, 1959; Elwes and Henry, 1908; Kondrat'eva-Melville, 1965). *Acer* has not been comprehensively monographed in this century, and the partial classification of Rehder (1940), slightly modified by Brizicky (1963), is followed here.

Despite the limitations of herbarium specimens for observations of shoot organization, it was evident from this survey that the maples can be conveniently grouped into four categories based on shoot growth and heterophylly:

FIGURE 7. First-year seedling of *A. rubrum* collected at Harvard Forest in late August.

FIGURES 8, 9. Developing long and short shoots of *A. rubrum* collected on same date (late May) from same tree. On the long shoot (FIGURE 8) three pairs of early leaves are nearly mature and two pairs of late leaves have unfolded. The growth of the short shoot (FIGURE 9), with two pairs of early leaves, is nearly complete.

(1) Species in this category, which possibly includes the majority in the genus, are like red or striped maple in the organization of the shoot system and the regular production of two kinds of leaves. Included here are the other species in sect. MACRANTHA, all closely similar to striped maple. More widespread in the genus is the red maple pattern: less sharply distinct long and short shoots, more than one early-leaf node on most shoots, and less abrupt changes in leaf shape on long shoots. This pattern is represented in sections CAMPESTRIA Pax, ARGUTA Rehd., and ACER (*Spicata* Pax). It is also present in *A. pycnanthum* K. Koch, a Japanese maple in sect. RUBRA which closely resembles red maple in most of its characteristics. Members of group (1) are considered in more detail below.

(2) This group has the same kind of shoot organization as (1), but epigenetic leaves of long and other types of shoots do not differ as consistently in size and shape from leaves preformed in buds. Included here are maples in sections RUBRA (*A. saccharinum* L.) and ACER (*A. spicatum* Lam., *A. caudatum* Wall.).

(3) In this group the shoot system is not organized into long and short shoots, and the elongate shoots of the crown are known or inferred to be mostly preformed in the bud. But leaves that develop epigenetically, when they are produced at all, differ in form and size from preformed leaves. All of the species in section PLATANOIDEA Pax are included here.

Representative of this group are *Acer platanoides* and *A. miyabei* Maxim. Many elongate shoots of these maples bear only 3 to 4 pairs of leaves, but the most vigorous produce 1 to 3 additional pairs of smaller, differently shaped leaves crowded at the shoot tip. On such shoots of *A. miyabei* there was a distinct break in size and form between nodes 4 and 5 (FIGURE 12d, e). The upper leaves were smaller, with an elongate median lobe and reduced lateral lobes projecting at right angles from the midrib.

Acer platanoides shows the same tendencies in leaves at the tips of elongate shoots in the crown, on sprouts, on lammas and disguised lammas shoots of young trees, and on the weak sylleptic shoots that often develop at the upper leaf-node of flowering shoots in this and other maples. The first seedling leaves are usually unlobed or obscurely lobed, but on many first-year seedlings they are followed by a disguised lammas shoot (Kondrat'eva-Melville, 1965: *Figure 3*), with small leaves which are similar in shape to epigenetic leaves produced at later stages of development.

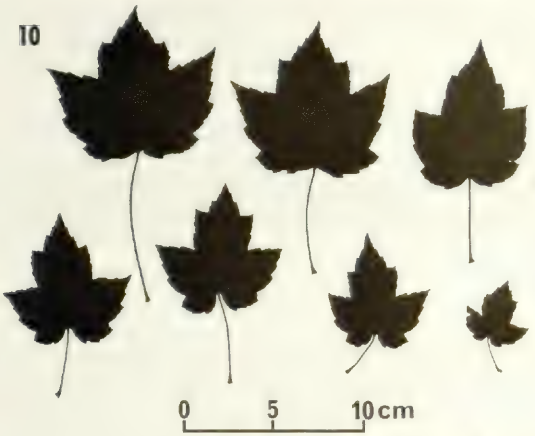
(4) The shoot system of this group is organized like that of (3), but the differences in size and shape between preformed and other leaves are less consistent. Sections SACCHARINA Pax (including *A. saccharum*) and PALMATA Pax are in this category. The leaves of individual sugar maples are fairly uniform in shape, and even sprout leaves are not always markedly different. The first pair of leaves of *A. saccharum* seedlings are unlobed or nearly so, but additional leaves produced during the first season may be shaped much like leaves produced at later stages.

Of the many maples in category (1), the largest aggregation of related species is sect. MACRANTHA, which includes 15 to 20 Asian species in addition to *Acer pensylvanicum*. Their classification is based almost entirely on differences in size and shape of early leaves; the reproductive structures are rather uniform and do not provide many useful distinctions (Rehder, 1933).

The Asian species are nearly identical to striped maple in the organization of their shoot systems. Throughout the section, the short shoots have a single pair of early leaves which vary in shape from 3- or 5-lobed to unlobed in different species. The long shoots bear, in addition, one or more pairs of smaller late leaves, and internode 2 is the longest on most shoots (FIGURE 12c). In species with lobed leaves, the differences in shape between the two kinds of leaves are much like those in striped maple: the late leaves have relatively elongate median lobes and shortened, basally displaced lateral lobes (FIGURE 11b: *A. rufinerve* Sieb. & Zucc.; FIGURE 12a, e: *A. tegmentosum* Maxim., *A. capillipes* Maxim.). In some species the angle formed by the lateral veins is consistently larger in late leaves (e.g., *A. grosseri* Pax: 65–82° in early leaves *vs.* 92–106° in late leaves). The trend toward reduced lobing is sometimes reversed in species with unlobed or obscurely lobed early leaves, and the late leaves may have small lateral lobes at the base of the blade. Throughout this section, the marginal serrations of late leaves tend to be fewer, coarser, and blunter.

Apart from leaf shape, the other maples in section MACRANTHA differ from striped maple primarily in their smaller vegetative structures. Only *A. tegmentosum* approaches it in leaf, internode, and bud size. In the other species, both kinds of leaves are smaller, the vegetative short shoots average 1 to 1.5 cm. and rarely exceed 3 cm. in length, and the longest internodes of most long shoots are only 8 to 12 cm.

Also included in group (1) are most or all of the maples in sect. CAMPESTRIA Pax. (Possible exceptions are *A. opalus* Mill. and *A. hyrcanum* Fisch. & Mey., for which adequate material was not available). The organization of the shoot system is much like that of red maple, with 1 to 3 pairs of early leaves on all shoots originating from buds. Long shoots are regularly produced, and heterophylly is pronounced (FIGURE 11c, e, f), but the differences between early and late leaves vary greatly between species. *Acer campestre* L., like many other maples, has late leaves with short petioles (FIGURE 12b) and basally displaced lateral lobes (12e) which project from the midrib at large angles (12d). Unlike the late leaves of most other maples, however, they often have more lobes and blunt teeth than the early leaves. This tendency is more conspicuous in *A. monspessulanum* L., in which the more numerous lobes and teeth of the late leaves are the most reliable distinction between the two kinds of leaves (FIGURE 11e). The opposite is true of *A. orientale*, a Mediterranean species with small leathery leaves. The lateral lobes of its late leaves are much reduced in size (FIGURE 11f), and the first pair on long shoots may lack lobes or teeth.



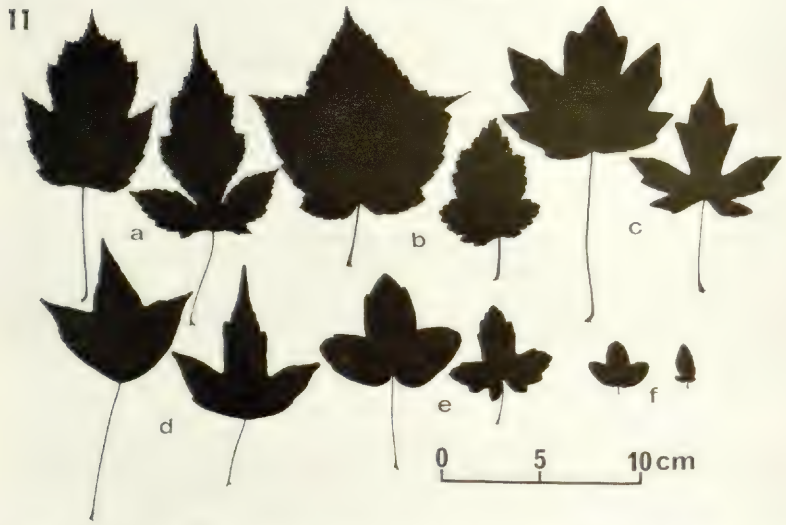


FIGURE 10. Mature leaves of a long shoot of *A. rubrum* (one leaf per node). Early leaves in upper row, node 1 at left.

FIGURE 11. Early and late leaves of *Acer* species: a. *A. tataricum* (nodes 2, 5), b. *A. rufinerve* (1, 3), c. *A. campestre* var. *leiocarpum* (2, 5), d. *A. buergerianum* (2, 7), e. *A. monspessulanum* (1, 8), f. *A. orientale* (1, 4). Leaves in a, c, and d from shoots illustrated in FIGURE 12.

The species in section ARGUTA also conform closely to the red maple pattern of shoot organization. They have a maximum of two or three early leaves per shoot, depending on the species. The expression of heterophylly in *A. barbinerve* Maxim. is typical of this section and similar to many other maples. Its late leaves have shorter petioles (FIGURE 12b) and smaller, basally displaced, projecting lateral lobes (FIGURE 12a, d, e).

Acer section ACER (*Spicata*), the most heterogeneous of Rehder's sec-

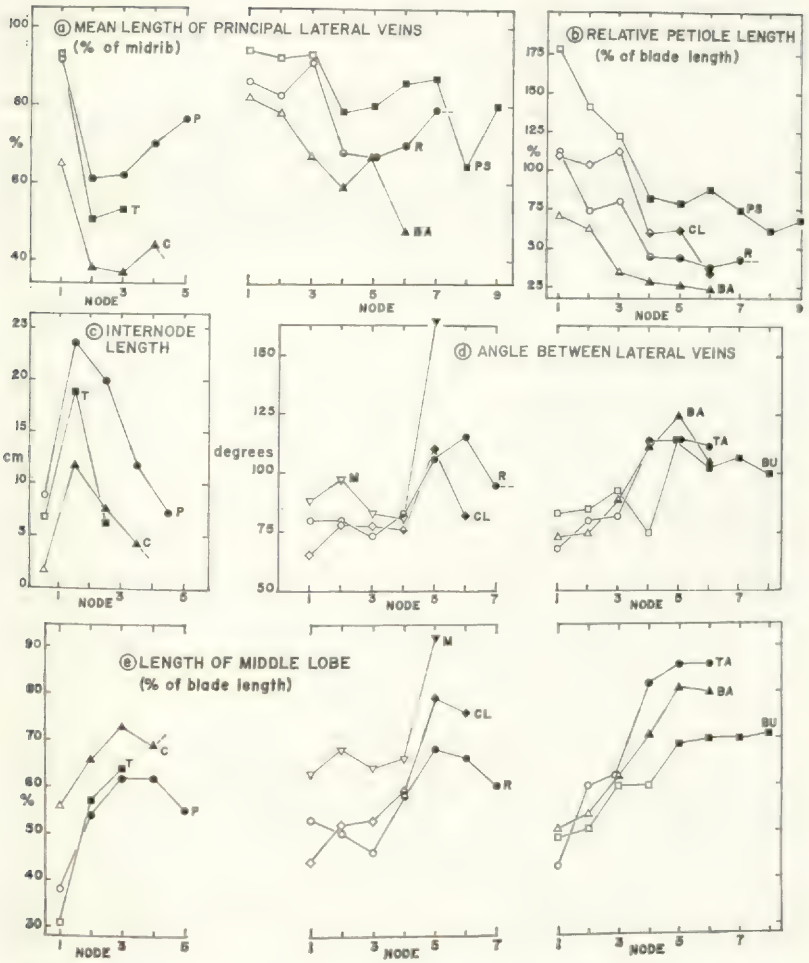


FIGURE 12. Variation in leaves and internodes on long shoots of *Acer* species: *A. barbinerve* (BA), *A. buergerianum* (BU), *A. campestre* var. *leiocarpum* (CL), *A. capillipes* (C), *A. miyabei* (M), *A. pensylvanicum* (P), *A. pseudoplatanus* (PS; data from Schüepp, 1929), *A. rubrum* (R), *A. tataricum* (TA), and *A. tegmentosum* (T). Transitional and late leaves shown by half-black and all-black symbols. Uppermost leaf-nodes (not shown) were immature in *A. capillipes*, damaged by insects in *A. rubrum*.

tions, includes several taxa that conform in varying degrees to the red maple pattern: *A. pseudoplatanus*, *A. buergerianum* Miq., and the shrubby species-complex made up of *A. tataricum* L. and *A. ginnala* Maxim. Of these, *A. pseudoplatanus* appears to be least regular in the production of long shoots; extension growth of young trees is commonly prolonged by lammas and disguised lammas shoots (Späth, 1912; Burger, 1926). Long

shoots are most abundantly produced by the *A. tataricum-A. ginnala* complex, and this abundance is a factor in their shrubby habit.

The expression of heterophylly in these members of section SPICATA follows the familiar maple pattern. Pearsall and Hanby (1926) observed that *A. pseudoplatanus* leaves produced during the summer were smaller and more dissected, with reduced basal lobes. They associated these morphological differences with increased water stresses. In the same species, the reduced lateral lobes of a long-shoot late leaf and a leaf of a sylleptic shoot were illustrated by Schüepp (1929: *Figure 16*). His data on a single long shoot shows a pronounced break between nodes 3 and 4 in the relative length of lateral lobes and petioles (FIGURE 12a, b). Schüepp's comparative observations of preformed and epigenetic leaf ontogeny make it clear that the lateral lobes of the preformed leaves appear earlier and are more nearly equal in size to the median lobe at subsequent stages of development. First-year seedling leaves of *A. pseudoplatanus* are either unlobed or have reduced lateral lobes (Elwes & Henry, 1908: p. 642).

Heterophylly is more pronounced in *A. buergerianum* and *A. tataricum* (FIGURE 11a, d). Both have late leaves with elongate median lobes and projecting lateral lobes (FIGURE 12d, e). One feature of *Acer tataricum* and its close relatives is unusual in this genus: the leaves at the first node are smaller than succeeding leaves, often unlobed, and occasionally almost devoid of serrations (Jackson, 1899: *Figure 33*).

DISCUSSION

The genus *Acer* is far more diverse than most woody genera in the organization of the shoot system and in the ways in which extension growth is prolonged after the expansion of the leaves and internodes laid down in the winter bud. In the many maples with some variation of long- and short-shoot organization, extension growth is ordinarily prolonged by the continued elongation of the long shoots after the spring flush of growth. Other maples, such as *A. saccharum* and to a large extent the species of section PLATANOIDEA, are much closer to the *Quercus-Fagus* type of shoot development. In these woody plants elongation stops, at least temporarily, after the expansion of the embryonic shoot in the winter bud. Prolonged extension growth of young trees tends to be discontinuous, through the repeated formation of lammas and (in maples) disguised lammas shoots (Späth, 1912).

The long shoots of red and striped maples, and by inference other maples with specialized shoots, originate in much the same way as those of *Populus trichocarpa* (Critchfield, 1960) and other woody plants of this type. Stem elongation is negligible if leaf production is confined to the relatively well-developed leaves of the winter bud. Only if additional leaves expand does appreciable elongation occur. The first of these added leaves may be present as primordia in the winter bud; in striped maple

the second set of leaves on long shoots sometimes consists solely of a single pair of late leaves originating from such primordia. More commonly, most of the leaves produced during the second phase of long-shoot development are initiated and expand during the same season.

In some woody plants with long and short shoots, this causal relationship between the production of a second set of leaves by some shoots and the elongation of those shoots appears to be mediated by auxin or auxin precursors produced by the developing leaves. The evidence for this interpretation, including the relative auxin production of long and short shoots in *Ginkgo biloba* (Gunckel & Thimann, 1949) and *Cercidiphyllum japonicum* (Titman & Wetmore, 1955), has been reviewed elsewhere (Critchfield, 1960). The work of Zimmermann (1936) on the production of auxin by *Acer pseudoplatanus* shoots supports the extension of this interpretation to maples with specialized shoot systems. Zimmermann did not discriminate between long and short shoots, but his data and photographs show that long shoots with about eight leaf-nodes, sampled in late June, had much higher levels of auxin than any shoots sampled earlier in the season. Zimmermann also found a fairly close relationship between internode length and auxin content in developing long shoots of this maple.

The stems of maple short shoots usually exhibit a limited but measurable amount of elongation, unlike those of some woody plants with specialized shoots. *Ginkgo biloba*, for example, produces short shoots only 1 to 2 mm. long. The leaf complement of red maple short shoots ranges from one to three pairs, and the presence of each additional pair is associated with small but consistent increases in stem length. These increments of stem growth are of a different order of magnitude, however, than those associated with late-leaf production. This is best illustrated by striped maple, in which the distinction between short and long shoots is reduced to the simplest possible terms. If a shoot produces only a single leaf-node it elongates an average of only 2 cm., despite the large size of the leaves. But the expansion of a single pair of late leaves, although they are only 1/10 to 1/3 the size of the early leaves, produces a stem averaging nine times as long. This great discrepancy between leaf size and stem length — 30- to 90-fold — illustrates one of the principal questions concerning plants with specialized shoot systems: why the elongation of short-shoot internodes is either limited (striped maple) or nonexistent (*Ginkgo*).

Red and striped maples, despite their similarity in shoot organization, differ greatly in potential leaf production per shoot. The greater potential of red maple is due partly to the nearly synchronous expansion of 2 to 3 pairs of preformed leaves, but a more important factor is its short late-leaf phyllochron — less than half of the 2-week interval of striped maple growing in the same environment. At an average rate of leaf development, a long shoot of red maple in the Harvard Forest could produce 17 leaf pairs by mid-September. An average shoot of striped maple could produce only eight pairs in the same period. However, because striped maple has larger leaves and longer internodes, it is estimated that its 8-

node shoot would exceed the 17-node shoot of red maple by at least 50 percent in both stem length and photosynthetic area.

In addition to the foliage leaves, maple shoots periodically produce another type of appendage, the bud scales. From comparisons of foliage-leaf and bud-scale ontogeny in *Acer platanoides* and other woody plants Goebel (1905) concluded ". . . the path of development is originally the same for all leaves, but in many leaves at an earlier or later period the development may proceed along different paths." His interpretation is equally applicable to the early divergence in development of preformed and epigenetic leaves of *Acer*, as Schüepp (1929) showed in *A. pseudoplatanus*.

Of the ontogenetic alternatives represented by early and late leaves, the development of leaves at the tip of a growing shoot is much more general. Leaves preformed in winter buds are produced only during the post-seedling growth of perennial plants. They develop in the very different microenvironment of the enclosed bud, and their ontogeny is sharply discontinuous, unlike that of epigenetic leaves. The first phase is a prolonged, well-defined period of what Sachs (1893) called "morphologische Ausgestaltung" (putting-into-shape), during which the form of the leaf is determined. The shape of the first leaves in the winter buds of *Acer palmatum* Thunb. is fully blocked out by the time they are 0.5 mm. long, and undergoes little change during later development (Meijknecht, 1955). The embryonic phase of preformed leaves, as Sachs pointed out, is separated from their expansion phase by a sharp boundary imposed by winter dormancy.

The degree of heterophylly associated with these two developmental patterns varies greatly between species of *Acer*, although the same morphological trends are present throughout the genus. *Acer saccharinum*, a close relative of red maple, regularly produces long shoots with late leaves that differ only subtly from the early leaves at the base of the same shoot. In most maples, however, the two kinds of leaves are distinct in size and shape, and maples with specialized shoot systems have both kinds present in the crowns of most trees.

The prevalence of this type of heterophylly in *Acer* has caused fewer taxonomic difficulties than might be expected. The main reason for this appears to be the sampling bias mentioned earlier. The great majority of herbarium specimens are flowering or fruiting shoots associated with only preformed leaves; foliage of elongate vegetative axes is under-represented or absent. Some taxonomic descriptions and keys are based explicitly on the leaves of fertile shoots only. Despite their limitations, they are probably more useful than those diffuse descriptions which attempt to encompass the range of nongenetic variation in leaf characters without recognizing its nature.

This failure to recognize and deal with heterophylly in woody plants has imposed unnecessary restrictions on the scope and usefulness of classification. Even in the context of the herbarium, it is often difficult or impossible to identify the occasional vegetative specimen lacking early

leaves, usually a segment of a long shoot or sprout. Yet the characteristics of other leaf types, and the organization of the shoot system itself, could be of considerable intrinsic value in classification. One of the most distinctive and unifying features of section MACRANTHA, for example, is the presence of a single pair of leaves on all short shoots. The regular production of heterophyllous long shoots by *Acer campestre* argues against its proposed transfer to section PLATANOIDEA (Brizicky, 1963), which lacks this type of shoot organization. Apart from this taxonomic potential, the recognition and exploitation of heterophylly and shoot characteristics in the classification of such woody genera as *Acer* would increase the value of taxonomic information in such related fields as ecology and paleobotany, which necessarily deal with whole-plant variability.

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THE POLYGALACEAE IN THE SOUTHEASTERN UNITED STATES[1]

NORTON G. MILLER

POLYGALACEAE R. Brown in Flinders, Voy. Terra Austr. 2: 542. 1814. "Polygaleae," nom. cons.

(MILKWORT FAMILY)

Annual or perennial herbs [spiny shrubs, sometimes small trees or climbers] with taproots, rarely rhizomes. Leaves alternate or whorled, simple, scalelike in some, entire, exstipulate [petioles biglandular in a few]. Inflorescences axillary, terminal [or extra-axillary] racemes and panicles, rarely otherwise. Flowers bracteate, perfect, zygomorphic [rarely subzygomorphic to actinomorphic], both chasmogamous and cleistogamous types infrequently present. Sepals [4] 5, persistent in fruit or caducous, free, or the abaxial pair fused [or the calyx ± synsepalous], the inner (lateral) segments (wings) petaloid and larger than [or ± equal] the others. Petals 3 [5, or if 3, 2 additional rudimentary petals often present], in most incompletely fused to form a tube in which the adaxial margins of the upper two segments overlap, the abaxial petal (keel) fimbriate-crested or not, sometimes lobed, the corolla caducous. Stamens 8, rarely [4 or 5] 6 [7 or 8–10], filaments mostly united, the resulting sheath connate with the corolla below, but split above; anther sacs 2, dehiscence usually ± porocidal [sometimes by longitudinal slits], introrse, the opening generally subterminal, oblique; pollen polycolporate,

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, Carroll E. Wood, Jr., principal investigator). The present treatment follows the plan initiated in the first contribution of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area dealt with includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. Descriptions are based on species occurring in this region, with additional information from extra-regional taxa in brackets. Ranges of the species mentioned are derived mostly from specimens examined and partly from data already published. I have checked distribution patterns against material available in the Herbarium of the University of North Carolina at Chapel Hill and am grateful for access to this collection. References followed by an asterisk are those which I have not been able to check for accuracy of citation.

My thanks are extended to Dr. Wood for his continuing assistance and advice, to Mrs. Nancy Dunkly who has helped with bibliographic problems and prepared the final typescript, to Dr. Lily M. Perry for providing some much appreciated help in the library, and to Dr. R. W. Long for sending a copy of the treatment of the Polygalaceae from his soon-to-be-published flora of subtropical Florida. The illustrations are the work of Miss Virginia Savage, and, for the most part, are based on preserved material obtained through the courtesy of R. B. Channell, R. A. Howard, the late H. F. L. Rock, S. J. Smith, and C. E. Wood, Jr.

often synorate, exine stratification obscure, polar axis 25–62 μ. Ovary superior, sessile [rarely stipitate], [1]2[3, 4, 5, or 7 or 8]-locular, hypogynous nectary present [or absent, sometimes annular]; style one, central, apical, usually curved, the apex 2-lobed [simple, or otherwise], one lobe stigmatic, the other often ending in a tuft of hairs; ovules one [rarely more] in each locule, pendulous from the ovary apex near the septum, anatropous to hemianatropous, crassinucellar, bitegmic, both integuments forming the micropyle. Fruit a loculicidal capsule [or drupe, nut, or samara]. Seeds often hairy [sometimes comose], generally with a fleshy micropylar aril or a harder outgrowth; endosperm usually present, fleshy; embryo straight, cotyledons orbicular, linear [or foliaceous]. Embryo sac development usually of the Polygonum type; embryogeny of the Asterad type. TYPE GENUS: *Polygala* L.

A nearly cosmopolitan family of about 15 genera and 800 species in three tribes, two monotypic. With about 50 species of *Xanthophyllum* Roxb., trees and shrubs mainly of the Indomalayan region, the Xanthophylleae Chodat (calyx and corolla separate, stamens free or only partially fused, ovary 1-locular, placentation parietal) occupies a somewhat anomalous position in the Polygalaceae and is occasionally treated as a separate but allied family. Perhaps the most advanced tribe of the family, the Moutabeae Chodat (calyx and corolla united, filaments fused into a split sheath, ovary 2–8-locular, placentation axile), contains only *Moutabea* Aubl., a small genus of tropical South American shrubs. In addition to *Polygala*, two other genera of tribe Polygaleae (calyx and corolla separate, filaments fused into a split sheath, ovary 2-locular, placentation axile) are found in North America: *Securidaca* L., fruits indehiscent, dry, 1-seeded samaras, and *Monnina* Ruiz & Pavon, fruits 1- or 2-locular, drupaceous, or dry and surrounded by a membranaceous wing. Species of *Securidaca* are principally climbers and occur throughout the tropics; *Monnina* is strictly New World in distribution with species found from Chile northward to the southwestern United States (*M. Wrightii* A. Gray, from Durango northward to Arizona and New Mexico).

Members of the Polygalaceae have distinctive polycolporate pollen, which in at least one genus, *Diclidanthera* Mart., has helped to document its placement in the family. Self-pollination is known to occur in *Salomonia* Lour., a small Indomalayan and Australian genus of free-living and root parasitic herbs (Rao); *Muraltia* DC., a large genus of South African shrubs (Levyns, 1954); and *Polygala*. Included phloem has been recorded for species of *Bredemeyera* Willd., *Moutabea*, and *Securidaca*.

Reported chromosome numbers for six genera excluding *Polygala* are $2n = 10$, 14, 16, 18, 20, 22, 32, and 44.

Families considered related to the Polygalaceae on the basis of common anatomical characters include the Trigoniaceae, Tremandraceae, Zygophyllaceae, Malpighiaceae, and Vochysiaceae (Heimsch). Excluding the Zygophyllaceae and adding the Krameriaceae, these families comprise the Polygalales of Cronquist, which are regarded as an offshoot of the Sapin-

dales. Other authors suggest relationships to certain families or groups of families for the most part originally included in the Geraniales of Engler & Prantl.

Apart from certain species of *Comesperma* Labill., *Securidaca*, and *Polygala* that are sometimes cultivated as ornamentals, few other members of the family are of economic importance. Oil from seeds of *Xanthophyllum lanceatum* (Miq.) J. J. Sm., the siur tree of Sumatra, is used in native cooking and in Europe in the manufacture of candles and soap (Hutchinson).

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Polygala Linnaeus, Sp. Pl. 2: 701. 1753; Gen. Pl. ed. 5. 315. 1754.

Single- to many-stemmed, erect, ascending, or rarely creeping herbs [or unarmed to spiny shrubs] of open, dry or wet sands, moist peats, and, less frequently, damp, wooded sites. Roots usually aromatic, sparse in annual species, often taprooted, or with a slender, stoloniferous rhizome in perennials. Leaves simple, alternate or whorled, rarely subopposite, sometimes organized into a basal rosette, petioles short, blades generally ovate or lanceolate, or reduced to scales in some, entire, pubescent or glabrous, and often with glandular dots. Inflorescences loose to tight, terminal or axillary [rarely extra-axillary] racemes or corymbose panicles, flowers often aggregated into spikes or heads, rarely 1–4 on short, subterminal, axillary branches. Chasmogamous flowers zygomorphic, pedicellate, subtended by a persisting or caducous bract and two bracteoles: flower color white, pink, yellow, or orange, yellow flowers of some becoming blue-green upon drying. Sepals 5, quincuncial in bud, the wings large and petaloid, abaxial sepals 2, small, greenish, free or fused laterally for most of their length, adaxial sepal greenish, generally larger than either of the two abaxial segments, hooded in some; margins of abaxial and adaxial sepals often ciliate, sometimes bearing glandular hairs. Petals 3, the upper two fused to the abaxial petal (keel) along one margin, but free and overlapping above, or the lower margins of the upper two petals fused to the stamen sheath, which is connate basally with the keel; corolla often changing color with age. Stamens 8, rarely 6 in two groups of 3 each; anther sacs laterally confluent at anthesis, dehiscence subapical, ± porocidal, or by a V-shaped slit on the inner face of the anther wall. Ovary bicarpellate, compressed contrary to the septum, an

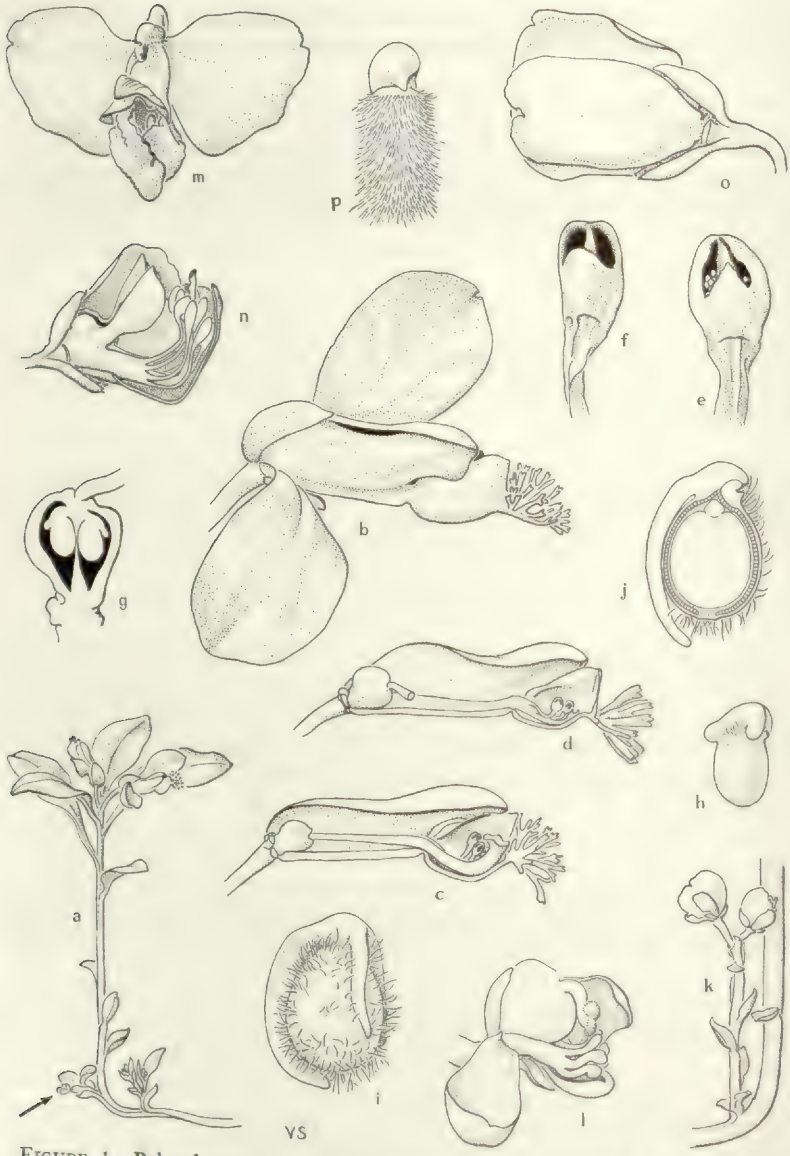

FIGURE 1. **Polygala** subg. **Chamaebuxus** and subg. **Hebeclada.** a–l, *P. paucifolia*: a, plant with two chasmogamous flowers and one cleistogamous flower (at arrow), × 3/4; b, chasmogamous flower, × 3; c, chasmogamous flower in lateral view, calyx and one-half of corolla removed to show androecium and gynoecium, × 3; d, same, style removed, × 3; e, anther shedding pollen, × 20; f, empty anther, × 20; g, ovary in longitudinal section, one ovule per locule, style mostly removed (semidiagrammatic), × 8; h, ovule and immature three-lobed aril, funiculus slightly exaggerated, × 15; i, mature seed with three-lobed aril, × 8; j, mature seed in longitudinal section, endosperm stippled, inner

abaxial or adaxial nectariferous gland often present; style usually 2-lobed, stigmatic lobe generally subapical, thin membranes borne on both sides of the style between or at the junction of the two lobes. Cleistogamous flowers of ± similar morphology borne on basal, rarely aërial, branches in a few. Fruit a 2-loculate, glabrous [or pilose], thin-walled, loculicidal [sometimes winged] capsule, often accompanied by the persistent calyx. Seeds ovoid, globose, or ampulliform, pubescent, rarely glabrous and finely tuberculate, usually bearing a 2- or 3-lobed aril at the micropylar end [a hilar appendage present in some]; cotyledons ovate or linear, endosperm continuous, fleshy. (Including *Asemeia* Raf., *Galypola* Nieuwl., *Pilostaxis* Raf., *Senega* Spach, *Triclisperma* Raf.). LECTOTYPE SPECIES: *P. vulgaris* L., see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 446. 1913. (A pre-Linnaean name from Greek, *polys*, much, and, *gala*, milk, in reference to a plant which was thought to increase lactation.) — MILKWORT.

A large (about 500 species), widely distributed genus (throughout Temperate and Tropical Zones, but absent from New Zealand, Polynesia, and the Arctic regions), well known for its small, usually brightly colored flowers. In North America the genus is best represented in the eastern part of the continent and in the southwestern United States and Mexico. It is largely absent from the dry, mid-continent region and the Pacific Northwest (*Polygala californica* Nutt. ex Torr. & Gray from central, coastal California to southwest Oregon only). Blake (1924) credits 31 species to the southeastern United States; Small (1933) accepts 37 species (in five genera) for the same area. Many are endemic to parts of this region; others occur northward or in the Caribbean region where the genus is also well represented.

In his *Monographia Polygalacearum*, Chodat (1893) proposed dividing *Polygala* into ten sections.[2] One of these has been renamed sect. PSEUDOSEMEIOCARDIUM Adema, a change necessitated by the demonstration that the type of sect. SEMEIOCARDIUM (Zoll.) Chodat (*Semeiocardium Arriensii* Zoll., which occurs on Madura and Kangean islands off northeast Java) is actually a member of the Balsaminaceae (see C. A. Backer,

[2] While unambiguously using the rank *sectio* in the monograph, Chodat refers to several of the sections as *sous-genres* in at least one prior (1889) and one subsequent (1913) work. However, there is no definite indication that he intended to use subgenus in the formal sense that it is now employed. Indeed, since *sous-genre* and *sectio* are freely interchanged on pp. 154 and 155 in the 1913 paper, they seem to have been employed as equivalent categories, as A. P. de Candolle and others had used them earlier (see G. K. Brizicky, Taxon 18:643–660. 1969).

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layer of seed coat hatched (semidiagrammatic). × 8; k, branch bearing two young capsules developed from cleistogamous flowers. × 2; l, cleistogamous flower, perianth and androecium pulled away from style (see text). × 10. m–p, *P. grandiflora*: m, flower at anthesis. × 6; n, flower in lateral view, one sepal (wing) and part of the corolla removed. × 6; o, fruit in lateral view, one sepal (wing) removed. × 6; p, arillate seed. × 10.

Gard. Bull. Singapore 9: 70–72. *1 pl.* 1935). Blake's classification (1916) in which many of Chodat's sections are treated as subgenera expresses the morphological diversity of the genus better. In the region covered by the *North American Flora*, Blake (1924) later recognized 13 infrageneric categories (including *Badiera* DC., subshrubs with subequal sepals, predominantly of West Indian distribution) whose rank, unfortunately, was not indicated.

Species belonging to three subgenera are found in the southeastern United States. Only one member of subg. CHAMAEBUXUS (DC.) Blake (keel cristate, calyx caducous, abaxial sepals separate), *Polygala paucifolia* Willd., fringed polygala, flowering wintergreen, occurs in our area or elsewhere in eastern North America, although species assigned to this subgenus are known from the southwestern United States. A plant of wide but somewhat sporadic distribution, typically found in moist, deciduous forests, this species ranges from Quebec (Anticosti Island and Gaspé County), southward through parts of New England, New York, and Pennsylvania and along the mountains to northern Georgia (including a few stations in western North and South Carolina and eastern Tennessee). It extends westward across southern Ontario (as far north as James Bay), Michigan, northern Wisconsin, and Minnesota to southern Manitoba and central Saskatchewan.

Differing from our other species of *Polygala* in having six rather than eight stamens, an obscurely bilobed stigma lacking a tuft of hairs, an adaxial nectariferous gland, and seeds with three-lobed arils, *P. paucifolia* appears to be closely related to certain other members of the subgenus, particularly the European *P. Chamaebuxus* L. In *P. paucifolia*, minute cleistogamous flowers are produced on short, erect branches that originate near the base of the upright leafy shoot (see FIGURE 1, a, k, l) and less frequently, later in the summer following disappearance of fruits developed from the chasmogamous flowers, at the apex of the plant or from axils of reduced leaves along the leafy shoot. While agreeing in general structure with the chasmogamous flowers, those of the cleistogamous type have a downward flexed, shortened style with an obviously two-lobed stigma, lack a crested keel, and have their stamens fused into two groups of three each, one unit borne on either side of the ovary and free from the corolla. Leaf-bearing branches of *P. paucifolia* overwinter and are replaced in the spring with foliage developing on a new shoot produced from the shallow rhizome.

Subgenus HEBECLADA (Chodat) Blake (keel ecristate, calyx persistent in fruit, abaxial sepals connate) is represented with us by *Polygala grandiflora* Walt., $2n = 28$, which ranges along the Coastal Plain (rarely at Piedmont localities) from southeastern North Carolina to Florida and westward to Mississippi. Members of this subgenus occur otherwise in South and Central America and in the West Indies. Specimens referable to *P. grandiflora*, particularly from southern Florida, vary greatly in leaf shape, flower color, and vesture. Several varieties have been distinguished in this region (see Blake, 1924), including var. *angustifolia* Torr. & Gray,

with linear or narrowly linear-lanceolate leaves (*vs.* narrowly lanceolate to elliptic in var. *grandiflora*, which probably includes *P. cumulicola* Small and *P. miamiensis* Small, both described from collections made in Dade County, Florida) and var. *leiodes* Blake, with glabrous or sparsely pubescent, linear leaves and sepals lacking nonglandular hairs. While accepting these varieties, Long stresses dark purple wings (*vs.* greenish or purplish in the others) as the distinguishing character of var. *leiodes*. These characters are often difficult to correlate in herbarium specimens, and the *P. grandiflora* complex in Florida remains perplexing and in need of further study.

Our other species, about 30 in number, belong to subg. Polygala (subg. *Orthopolygala* (Chodat) Blake, keel cristate, calyx persistent in fruit, abaxial sepals separate), which contains at least three-quarters of the species in the entire genus. Although Chodat (1893) provides a lengthy classification of the species in his sect. Orthopolygala, some of the categories adopted appear unnatural (e.g., "Senegae," containing *Polygala Senega* L. and *P. polygama* Walt.), while others contain clearly related species (e.g., "Decurrentes," comprised of *P. lutea* L., *P. Rugelii* Shuttlw. ex Chapm., *P. nana* (Michx.) DC., *P. cymosa* Walt., *P. ramosa* Ell., and *P. Balduinii* Nutt.). Small (1933), treating only those species found in our area, recognized a monotypic genus, *Galypola* Nieuwl., for *P. incarnata* L., *Pilostaxis* Raf. for species in the Decurrentes, and kept the residuum in *Polygala* in which seven informal, although named, categories were presented. The characters used to distinguish the two genera are minor and seem better utilized at some infrageneric rank.

Eight, possibly more, endemic species belonging to subg. Polygala occupy portions of the Southeast. Known only from Florida are *Polygala Lewtonii* Small, with cleistogamous flowers, according to Blake (1924), reported from the sandy *Pinus clausa* scrub areas in the central part of the state (Highlands, Lake, Marion, Orange, and Polk counties) and *P. Rugelii*, $2n = 68$, which grows on wet, sometimes peaty sands throughout the Florida peninsula. Others, less restricted in distribution, and found mainly at places along the Coastal Plain, include *P. Balduinii* Nutt. (possibly conspecific with *P. Carteri* Small, from southern Florida, but this problem needs further study), *P. setacea* Michx., *P. crenata* James, with cleistogamous flowers borne on basal, leafless branches, *P. Chapmanii* Torr. & Gray, $2n = 72$, *P. leptostachys* Shuttlew. ex A. Gray, *P. Boykinii* Nutt. var. *Boykinii*, $2n =$ ca. 28, and from south Florida only, *P. Boykinii* var. *sparsifolia* Wheelock (which probably includes *P. flagellaris* Small and is presumably the same as *P. praetervisa* Chodat, $2n = 96$, since the types cited by Wheelock and Chodat are portions of the same collection).

The more widespread, nonendemic species have ranges of several types. Occurring predominantly outside of the Southeast and found in various parts of this region are *Polygala leptocaulis* Torr. & Gray, a plant of damp meadows and low pinelands in Florida, Mississippi, and Louisiana, which otherwise occurs in Texas, parts of Central and South America, and at

FIGURE 2. **Polygala** subg. **Polygala.** a, b, *P. Senega*: a, habit of plant in flower, all mature stems except one removed, × 1/3; b, gynoecium from flower at antithesis, × 20. c, d, *P. incarnata*: c, inflorescence, flowers near the apex, fruits toward the base, × 1 1/2; d, seed with two-lobed aril, × 15. e–n, *P. lutea*: e, inflorescence, flowers near the apex, fruits toward the base, × 1 1/2; f, flower, × 8; g, flower in lateral view just prior to anther dehiscence showing arrangement of stamens about apical brush, perianth mostly removed, × 12; h, style apex with stalked stigma and brush from flower at same stage as that in g, × 25; i, style apex from older flower, stalked stigma bent toward the apical brush which collects the pollen, × 25; j, ovary in slightly oblique longitudinal sec-

places in the West Indies, and *P. alba* Nutt., $2n = 24$, ca. 72, and 104–108, which Blake (1924) credits to Louisiana and Wheelock to Arkansas, although specimens have been seen only from the region to the west (Puebla, Mexico, to Texas and Arizona, and northward to southern Saskatchewan). Other species of less restricted distribution in the Southeast, but which nevertheless occur mainly beyond our area, are *P. Senega* L., known primarily from calcareous sites from northern Maine across Ontario (north to the James Bay region) to western Alberta, and south to the Carolinas, Georgia, Tennessee, Arkansas, and South Dakota; *P. sanguinea* L., from Nova Scotia to southern Ontario and Minnesota, south to North Carolina, Tennessee, Alabama, Louisiana, Mississippi, and eastern Texas; and *P. verticillata* L. var. *verticillata* (*P. Pretzii* Pennell),[3] which ranges widely throughout the eastern United States and southern Canada south to Tennessee (Pennell, 1931) and Louisiana. Several varieties (some often treated as species) are usually recognized as distinct from var. *verticillata*. Those represented in our region (and also to the north) include *P. verticillata* var. *isocycla* Fern. (*P. verticillata* L. var. *verticillata* sensu Pennell), $2n = 34$, a plant of dry soils throughout the Southeast, *P. verticillata* var. *ambigua* (Nutt.) Wood, from North Carolina to Arkansas, at stations mostly inland from the Coastal Plain, and *P. verticillata* var. *dolichoptera* Fern., from Arkansas.

A second group of species, growing chiefly in savannahs or on wet, often peaty sands, ranges widely across the Gulf and Atlantic coastal plains, sometimes occurring west to eastern Texas and north to coastal New England. These are *P. Hookeri* Torr. & Gray, from North and South Carolina, Florida, and Louisiana (to Texas, Blake, 1924); *P. brevifolia* Nutt., from New Jersey, North Carolina, Florida, Alabama, and Mississippi; *P. nana* (including *P. arenicola* Small), $2n = 68$, from South Carolina (Lexington Co.) and Tennessee (Rhea Co.), Georgia, Florida (widespread), west to Louisiana, eastern Texas (and Arkansas, Blake, 1924); *P. ramosa*, $2n = 68$, from New Jersey (Small, 1933) and Delaware to Florida, west to eastern Texas; *P. cymosa*, from Delaware to Florida, west to eastern Louisiana; and *P. lutea* (with orange, rarely yellow flowers), $2n = 68$, from Long Island to Florida, west to eastern Louisiana.

The third group, species found both at Coastal Plain localities and more or less widely in the interior of the continent, includes the following: *P. polygama* Walt. (including *P. aboriginum* Small, according to James),

[3] See Fernald (1938) and Pennell (1933 & 1939) for two different views on the interpretation of the Linnaean type of this species.

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tion, at left, ovule with immature aril, at right, ovule showing funiculus (semidiagrammatic), × 20; k, ovule with immature two-lobed aril, × 25; l, fruit and persistent calyx, corolla fugacious, × 6; m, seed with two-lobed aril, × 25; n, seed in longitudinal section, endosperm stippled, inner layer of seed coat hatched (semidiagrammatic), × 25. o, *P. nana*, arillate seed, × 25. p, *P. ramosa*, arillate seed, × 25. q, *P. cymosa*, seed, aril minute or wanting, × 25.

$2n = 56$, with aërial (Robinson, Shaw) or subterranean racemes of cleistogamous flowers, distributed from Nova Scotia to Florida, west to Texas, and at scattered localities inland on dry sandy soils from southern Ontario to Minnesota, south to Arkansas and northern Georgia (northern and inland material often referable to var. *obtusata* Chodat, $2n = 56$); *P. incarnata* L. (*Galypola incarnata* (L.) Nieuwl., our only species with the corolla at least twice as long as the wings), from Long Island to Florida, west to Texas, and inland sporadically to Wisconsin, Iowa, Kansas, and Oklahoma; *P. cruciata* L. (including *P. ramosior* (Nash ex Robinson) Small), $2n = 36$, with a distribution pattern similar to the preceding species, except inland (lake margins, meadows, peaty soils) to only the Upper Great Lakes region (Minnesota, Wisconsin, Michigan), and southward at scattered places in Illinois, Indiana, Ohio, Kentucky, Tennessee, and Alabama (most collections from the north, both coastal and inland, are referable to var. *aquilonia* Fern. & Schub.); *P. Curtissii* A. Gray, $2n = 40$, from Delaware to Georgia and Alabama, but less frequent southward along the Coastal Plain, although occurring inland from northern Alabama and Georgia, north to Ohio and West Virginia; *P. Nuttallii* Torr. & Gray, $2n = 46$, from Massachusetts south to North Carolina and Georgia, inland to Tennessee and Kentucky (also Alabama, Mississippi, and Arkansas, Blake, 1924, Small, 1933); and *P. mariana* Mill. (possibly including *P. Harperi* Small, which according to Fernald, Gray's Man. Bot. ed. 8. 956. 1950, ranges from southeastern Virginia to Florida, west to eastern Texas), $2n = 34$, from New Jersey to Florida, west to eastern Texas, Arkansas, and Tennessee.

Relatively little recent work on the anatomy and morphology of the genus has appeared. Holm mentions the occurrence of lysigenous oil ducts and oil drops in cortical and epidermal cells and discusses briefly certain other aspects of vegetative structure for some of the species found in our region. The morphology of the style and stigma, which varies somewhat from the basic two-lobed situation among the species studied by Holm, seems constant enough within certain groups of species to be useful in developing a future infrageneric classification. Anther walls in several Indian species (Venkatesh) are comprised of epidermal, hypodermal, middle, and tapetal layers. Cells of the hypodermis have fibrous bands that originate from a common point on the inner tangential wall, extend along the radial walls to terminate on the outer tangential wall. Shrinkage of the fibrous cells ruptures the anther wall in a predetermined zone on its inner, subapical surface. The occurrence of partially or entirely tetrasporangiate stamens in individual flowers of certain species indicates that the bilocular stamens of *Polygala* are derived by suppression of the two abaxial microsporangia.

The pollination mechanism in species of *Polygala* is an interesting but little studied subject. Venkatesh's work indicates that autogamy may commonly occur. In the Indian species investigated, self-pollination is facilitated by a curving of the style which brings the stigma into close contact with the pollen that accumulates in a special pocket on the style.

However, whether these species are proterogynous or proterandrous, and therefore suited to cross-pollination as well, was not mentioned. In many of our species self-pollination seems to occur also but by a somewhat different mechanism. For example in *P. lutea*, the apical stigmatic lobe ends in a tuft of hairs which catches pollen shed from the eight tightly surrounding anthers (FIGURE 2, g). At this stage the stigmatic lobe is bent away from the pollen mass and toward the base of the style (FIGURE 2, h). Later, as the flower ages, the stigmatic lobe is reoriented so that the stigmatic surface is presented to the accumulated pollen (FIGURE 2, i). Within a single flower, however, the relationship between the time of anther dehiscence and the period of stigma receptivity is not known precisely, so it is possible that the stigma is receptive at the time pollen is shed, and autogamy occurs only if cross-pollination by insects has not. Observations on living plants need to be made.

The relatively large flowers of *Polygala paucifolia*, in contrast, seem especially suited to bee pollination, which has been described for the related *P. Chamaebuxus* (Faegri & van der Pijl). The two lateral, petaloid sepals and the keel of these species (and other members of the Polygalaceae) are analogous to the wings (alae) and standard (vexillum) of papilionaceous legumes, and the pollination mechanism in certain members of both families has much in common. A bee in search of nectar produced at the base of the ovary contacts the rigid style after forcing down the hinged, bowl-like apical appendage of the keel. In *P. paucifolia* this is crested and perhaps acts as a landing pad. Pollen accumulated on the horizontal surface at the end of the style is deposited on the underside of the insect, which leaves behind foreign pollen obtained from previously visited flowers.

Outgrowths at the micropylar end of the ovule, usually termed "arils," but perhaps more properly called arillodes (see L. van der Pijl, Acta Bot. Neerl. 6: 618–641. 1957), since they develop from tissues of the outer integument (Bresinsky), not from either the funiculus or the hilum, may be of diagnostic size and shape in certain species. These two- or three-lobed structures, often composed of large, hyaline cells, are said to be important in local dispersal by ants that utilize their contents as a food source (Ridley).

Chromosome numbers have been reported for relatively few species of *Polygala*. Because few pollen mother cells are formed in each anther and the chromosomes are small and often numerous, good meiotic figures are hard to obtain. Other counting difficulties arise during meiosis which is characterized by a prolongation of prophase I and rapid completion of the stages between prometaphase I and telophase I and of the phases of meiosis II (Lewis & Davis). Speciation through polyploidy, aneuploidy, and perhaps hybridization is suggested by the reported chromosome numbers: $2n$ = 14, 16, 18, 24, 28, 30, 32, 34, 36, 38, 40, 42, 44, 46, 48, 52, 56, 68, 72, ca. 84, 96, and 104–108, with $2n$ = 34 being the most frequently obtained count (9 spp.).

The genus is of little commercial importance. Several species, includ-

ing *Polygala myrtifolia* L., from South Africa, *P. paucifolia*, and *P. Chamaebuxus*, are sometimes cultivated as ornamentals, and preparations containing saponins from the thick, fleshy root of *P. Senega* are used medicinally as expectorants for treatment of various forms of bronchitis and asthma. Until recently, most senega root came from Manitoba and Saskatchewan, Canada (Gillett). The species is cultivated in Japan and India for its roots; elsewhere naturally occurring stands are harvested. *Polygala butyracea* Heck., from tropical Africa, is reported to be a source of fiber used locally for making cloth and other items (Hutchinson).

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EMBRYOLOGY OF THE MAGNOLIALES AND COMMENTS ON THEIR RELATIONSHIPS [1]

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COMMENTS ON FAMILIES

Austrobaileyaceae. The genus *Austrobaileya* has been included in Magnoliaceae (White, 1933), in Austrobaileyae, as a subfamily of the Dilleniaceae (Croizat, 1940), Monimiaceae (*see* Bailey & Swamy, 1949), or as a separate family Austrobaileyaceae (Croizat, 1943). According to Bailey and Swamy (1949) the presence of monocolpate pollen, ethereal oil cells, and absence of raphides negate any relationship with the Dilleniaceae. Since this genus has unilacunar nodes, it falls in category A of dicotyledonous families of Bailey and Swamy (1950) and thus has no close affinities with the Magnoliaceae. Bailey and Swamy (1949) remarked that the totality of evidence provides no justification for excluding *Austrobaileya* from Monimiaceae unless the concept of the family is narrowed to exclude such genera as *Trimenia*, *Piptocalyx*, and *Amborella* (*see also* Bailey & Swamy, 1948). However, in a subsequent paper discussing the relationships of the Monimiaceae (Bailey & Swamy, 1950) they include this genus in a distinct family, the Austrobaileyaceae, closely related to Monimiaceae.

Magnoliaceae, Degeneriaceae, and **Annonaceae.** Previously the Magnoliaceae included a number of genera of doubtful affinities like *Drimys*, *Schisandra*, *Illicium*, *Trochodendron*, *Tetracentron*, and *Euptelea* (*see* Bentham & Hooker, 1862–67; Engler & Prantl, 1887–1909; Hutchinson, 1959; Rendle, 1952). Dandy (1927) has circumscribed the family to include ten genera. Kapil and Bhandari (1964) have compared morphological and embryological characters of Magnoliaceae, *Schisandra*, and Illiciaceae and supported the removal of *Schisandra* and its allies to Schisandraceae, and *Illicium* to Illiciaceae (*see also* Bailey & Nast, 1948; Gifford, 1950; Lemesle, 1955; Ozenda, 1946; Smith, 1947). *Drimys* has also been rightly removed to a separate family, the Winteraceae (Bhandari, 1963; Bhandari & Venkataraman, 1968; Dandy, 1933; Smith, 1942, 1943; Van Tieghem, 1900). Similarly the removal of *Trochodendron* and *Tetracentron* (Bailey & Nast, 1945; Croizat, 1947; Nast & Bailey, 1945, 1946; Smith, 1945) and *Euptelea* (Lemesle, 1946; Nast & Bailey, 1946; Smith, 1946) to their representative family has been amply justified. The above conclusions are also corroborated by pollen morphology (Erdtman, 1952).

The family Degeneriaceae was established by Bailey and Smith (1942) and has been recognized as a distinct family of the magnolian stock (*see*

[1] Continued from volume 52, p. 39.

Eames, 1961), closely related to the Magnoliaceae and Himantandraceae (Bailey, Nast, & Smith, 1943; Swamy, 1949). Hutchinson (1959), however, considers that *Degeneria* is closely related to *Exospermum* and *Zygogynum* and should, therefore, be included in the Winteraceae. Bhandari (1963) has compared the morphological and embryological features of the Winteraceae and Degeneriaceae, and remarked ". . . *Degeneria* differs from the Winteraceae in many important features like the perianth, stamens, pollen grains, endosperm, embryo, seed coat and floral and vegetative anatomy, and is therefore, rightly placed in a separate monogeneric family, the Degeneriaceae (Bailey and Smith, 1942)." Swamy (1949) has concluded that Degeneriaceae, Himantandraceae, and Magnoliaceae are distinct but closely related families.

Bailey *et al.* (1943), Bailey and Smith (1942) and Swamy (1949) have pointed out that Magnoliaceae, Himantandraceae and Degeneriaceae are closely related. Eames (1961), however, maintains that the Annonaceae are most closely related to the Magnoliaceae and the two are perhaps derived from the same ancestral stock, whereas Eupomatiaceae, Himantandraceae, and Degeneriaceae are other families having affinities with the Magnoliaceae. In the absence of any embryological literature on the first two families Kapil and Bhandari (1964) have compared embryological, morphological, and anatomical features of the Magnoliaceae, Degeneriaceae, and Annonaceae and concluded that these families possess many common features such as the tree habit; multilacunar node; bisexual flowers (rarely unisexual in Magnoliaceae); embedded microsporangia; glandular tapetum with binucleate cells; monocolpate pollen (occasionally acolpate in Annonaceae) in which the generative cell is cut off towards the distal end; anatropous, bitegmic, and crassinucellate ovules; Polygonum type of embryo sac with ephemeral antipodal cells; cellular endosperm and follicular fruits. All these features strongly indicate their close relationship. At the same time they differ from each other in some important characters. The stamens are 1-traced in Annonaceae, 3-traced in Degeneriaceae and 3–7-traced in Magnoliaceae. In Magnoliaceae microspores are released from tetrads soon after their formation while they are retained in the tetrad till the differentiation of exine and colpi in the Degeneriaceae and in permanent tetrads in some members of Annonaceae; Ubisch granules are present in Magnoliaceae and not in the other two; the endosperm is ruminate in Degeneriaceae and Annonaceae but not in Magnoliaceae; sarcotesta is present in Magnoliaceae and Degeneriaceae but is absent in Annonaceae; instead a fleshy aril is found which is absent both in the Magnoliaceae and Degeneriaceae; follicles open by a dorsal suture in Magnoliaceae, by a ventral suture in Degeneriaceae, while in Annonaceae follicles become syncarpous in the fruit. The three families differ also in having varied basic chromosome numbers. In Magnoliaceae it is $n = 19$; in Degeneriaceae $n = 12$, while in Annonaceae it varies from $n = 7, 8,$ or 9. The family Himantandraceae resembles Degeneriaceae however, in possessing $n = 12$. It is therefore, quite evident that although these families are closely related they cannot be arranged in a linear phylogenetic sequence. They

have some features common to all, others overlapping with either of the families, and still others unique to each one. It may be concluded that they are closely related but distinct families of the magnolian complex.

Winteraceae. Bentham and Hooker (1862–67) recognized one genus *Drimys*, and along with *Illicium* placed it in the tribe Wintereae of the Magnoliaceae. Van Tieghem's (1900) was the first extensive survey of the family. He proposed the group Homoxylées to include all the vesselless dicotyledons and Drimyacées to comprise the five genera. *Pseudowintera*, the sixth genus, was added to the Winteraceae by Dandy (1933).

The Winteraceae have unique features such as the trends of specialization of the conduplicate carpel; the primitive stamen; permanent tetrads (elsewhere present only in the Lactoridaceae and Annonaceae) with pollen having the generative cell cut off towards the proximal face; extensive fibrous endothecium, monoporate pollen with conspicuous to minute reticulations; phenolic compounds in the outer epidermis of the outer integument; distinctive endosperm, embryo, and seed structure (*see also* Bailey & Nast, 1945).

Smith (1943a,b), however, agreed with Burtt (1938) in transferring *Tetrathalamus montana* from the Guttiferae but merged this genus with *Bubbia* as *B. montana* and therefore, recognized only six genera in the Winteraceae. Hutchinson (1959) and Barkley (1966) consider *Tetrathalamus* to be deserving of generic rank and the latter author further favors the recognition of *Wintera* and *Lassonia* (= *Magnolia*, *see* Willis, 1966) as winteraceous genera. Hutchinson (1959) is of the opinion that *Degeneria*, the monotypic genus of the Degeneriaceae (Bailey & Smith, 1942), is closely related to *Exospermum* and *Zygogynum* and should also be included in the Winteraceae.

Embryological information for *Tetrathalamus*, *Lassonia* and *Wintera* is lacking and therefore, any discussion pertaining to the taxonomic placement and relationship of these genera must await such data. Bhandari (1963) and Bhandari and Venkataraman (1968) have shown that *Degeneria* differs (Swamy, 1949) from the Winteraceae in many important aspects such as the perianth, stamens, pollen grains, endosperm, embryo, seed coat, and floral and vegetative anatomy, and they support Bailey and Smith (1942) in thinking this genus is rightly placed in a separate family, the Degeneriaceae, and deny any close affinities with the Winteraceae. Bhandari and Venkataraman (1968) considered that *Illicium* differs from the Winteraceae in having vessels in the xylem; unilacunar node; no differentiation in calyx and corolla; endothecium not extending towards the connective tissue; 2-layered glandular tapetum; pollen grains shedding individually, tricolpate pollen; closed sessile carpel; ephemeral antipodal cells; Asterad type of embryogeny; and seed structure. These dissimilarities obviously preclude any possibility of Winteraceae being related to *Illicium* and justify its separation to Illiciaceae (*see also* Bailey & Nast, 1945; Erdtman, 1952).

Cytologically also the family is distinct. The basic number x = 13 in the species of *Drimys* section Tasmania is similar only to that of *Illicium*

floridanum which is however of secondary origin by aneuploidy. No such evidence is available in Winteraceae. Secondly, the section WINTERA of *Drimys* and *Pseudowintera* have $n = 43$.

Taking into consideration the sum total of evidence from morphology, vegetative and floral anatomy (Bailey, 1944; Bailey & Nast, 1943a,b; 1944a,b; 1945; Nast, 1944), and embryology (Bhandari, 1963; Bhandari & Venkataraman, 1968; Sampson, 1963; Swamy, 1952), the Winteraceae form a distinct family of magnolian alliance but not closely related to any other existing family.

Myristicaceae and Canellaceae. The Myristicaceae is a homogeneous taxonomic unit. Because of the meager embryological information, not very dependable conclusions can be drawn. Joshi (1946), however, considers that the family is related to Annonaceae, and perhaps the ruminate endosperm and arillate seeds add further support to this conclusion.

The family Canellaceae has also been placed in either Parietales along with Violaceae, Bixaceae, Flacourtiaceae and Koeberliniaceae or in the woody Ranales near Myristicaceae, Illiciaceae, Schisandraceae, and Eupomatiaceae (Engler, 1964; Hutchinson, 1959). Wilson (1960) in a comparative study of wood anatomy concluded that the family is nearly related to Eupteleaceae, Eupomatiaceae, Illiciaceae, and Schisandraceae. Bessey (1915), Vestal (1935), and Wettstein (1935) regarded the families Myristicaceae and Canellaceae as closely related. Although the two families have a number of differences they also possess certain common features such as the simultaneous cytokinesis in the microspore mother cells; the generative cell cut off towards the proximal pole; anatropous, bitegmic, and crassinucellate ovules; Polygonum type embryo sac; ruminate endosperm; paratracheal parenchyma; and uniseriate rays. In both families the rays flare out in the phloem region. Parameswaran (1962) concluded that these two families have a greater degree of resemblance than the remaining families which possess ethereal oil cells, monocolpate pollen, and trilacunar nodes. However, one family cannot be derived from the other. Probably they had a common ancestral stock from which they deviated unidirectionally.

Schisandraceae and Illiciaceae. Most taxonomists, such as Bentham and Hooker (1862–1883), Engler and Prantl (1889–1897), and Rendle (1952) included *Schisandra* and *Kadsura* in a tribe, Schisandreae or a subfamily, Schisandroideae, of the Magnoliaceae. McLaughlin (1933), Whitaker (1933), Lemesle (1945, 1955), Ozenda (1946), Smith (1947), and Bailey and Nast (1948), on the basis of morphology, wood anatomy, and chromosome number, have concluded that Schisandreae should be raised to family rank as the Schisandraceae. This suggestion has been accepted and incorporated in most taxonomic treatments as that of Lawrence (1951), Hutchinson (1959), and Takhtajan (1966), Thorne (1968), and Cronquist (1968). On the basis of a comparative analysis of morphology, embryological and nodal structure of the Magnoliaceae, *Schisandra*, and Illiciaceae, Kapil and Bhandari (1964) pointed out that Magnoliaceae differs from *Schisandra* and Illiciaceae in having undifferentiated stamens with

1 to 7 traces and embedded microsporangia; bilayered glandular tapetum with binucleate cells; Ubisch granules; monocolpate pollen with smooth exine; unilocular ovary with 2 to 6 ovules; vascularized outer integument; testa differentiated into outer fleshy and inner stony regions; multilacunar and multitraced node; stipulate leaves; and $n = 19$ as the basic chromosome number; and supported the exclusion of *Schisandra* and *Kadsura* to their respective families (*see also* Kapil & Jalan, 1964). Bhandari and Venkataraman (1968) have shown that embryologically *Illicium* has no affinities with *Drimys* (*see also* Winteraceae) with which it was associated in the tribe Magnolieae of the Magnoliaceae (Bentham & Hooker, 1862–1868).

Kapil and Jalan (1964) evaluated the morphological, anatomical and embryological features of the Schisandraceae and Illiciaceae. The Schisandraceae possess the following characters in contrast to Illiciaceae: (a) climbers *vs.* trees or shrubs, (b) eustelic stem with well developed pericycle *vs.* pseudosiphonostele with poorly developed pericycle, (c) 3-traced unilacunar *vs.* 1-traced unilacunar node, (d) alternate leaves *vs.* pseudoverticillate, (e) haplocheilic stomata *vs.* syndetocheilic, (f) non-pitted sclereids with crystals *vs.* pitted sclereids without crystals, (g) unisexual *vs.* bisexual flowers, (h) spirally arranged carpels without style *vs.* whorled carpels with style, (i) stamens monadelphous *vs.* stamens free, (j) hexacolpate *vs.* tricolpate pollen, (k) embryo sac Polygonum, Oenothera or modified bisporic (*see* Swamy, 1964) type *vs.* Polygonum type, (l) Onagrad type of embryogeny *vs.* Asterad type, and (m) fruit a berry with succulent pericarp *vs.* fruit a follicle with sclerotic pericarp. They (Kapil & Jalan, 1964) concluded that these two families deviate in a large number of characters and there seems to be no close relationship between the Schisandraceae and Illiciaceae as suggested by Whitaker (1933), Smith (1947), and Bailey and Nast (1948). Eames (1961) proposes that Schisandraceae and Illiciaceae, though more specialized, are closely related to the Magnoliaceae and it is possible that all three families probably have been derived from a common ancestral stock. On the other hand, Smith (1947) remarked that *Illicium* has no close allies other than *Schisandra* and *Kadsura*; a conclusion corroborated by the chromosome number of $n = 14$. At the same time he emphasized that the two groups have specialized along different lines and have retained certain primitive features. It is impossible to indicate which is the more primitive. Smith's remarks made about two decades ago, and those of Eames (1961), and Bailey and Nast (1948) seem unfounded in the light of embryological investigations carried out recently. Further, the recent evidence from the karyotypic analysis for Illiciaceae (Stone & Freeman, 1968) and Schisandraceae (Stone, 1968) clearly indicates that Schisandraceae differs from Illiciaceae in having a nearly symmetrical karyotype and lacking subterminal chromosomes. It may very well be that Schisandraceae and Illiciaceae again represent the relics of the extant magnoliales much like many other families such as Winteraceae, Eupteleaceae, and Lactoridaceae.

Monimiaceae and allies. The Monimiaceae *sensu lato* included a large

number of genera having doubtful affinities such as *Amborella*, *Austrobaileya*, *Idenburgia*, *Scyphostegia*, *Trimenia*, *Piptocalyx*, *Calycanthus*, and *Gomortega* (*see* Money, Bailey, & Swamy, 1950).

According to Money *et al.* (1950) *Amborella* has characters resembling those of members of the Monimiaceae such as spiral arrangement of leaves, bracteoles, and tepals; the form and vascularization of the carpels; pollen morphology; fruit morphology; absence of ethereal oil cells; presence of multicellular hairs and hippocrepiform sclereids; and absence of pericyclic fibers in the stem. However, it differs in the orientation of anatropous ovules, narrow rays, and a single arc-shaped leaf trace. Therefore, its position in Amborellaceae, closely related to Monimiaceae, is justified (*see also* Bailey & Swamy, 1948).

Similarly *Trimenia* and *Piptocalyx* have been removed to a separate family, Trimeniaceae, *Gomortega* to Gomortegaceae, *Calycanthus* to Calycanthaceae and *Austrobaileya* to Austrobaileyaceae and all of these families are interrelated (Bailey & Swamy, 1940, 1949, 1950).

Embryological information on Amborellaceae, Trimeniaceae, and Gomortegaceae is not available, and the embryological literature on Monimiaceae itself is not sufficiently extensive to draw dependable conclusions. However, the Monimiaceae, Calycanthaceae, and Hernandiaceae resemble each other in having the successive type of cytokinesis in the microspore mother cells; periplasmodial tapetum (occasionally glandular in Monimiaceae); anatropous, bitegmic (also unitegmic in Monimiaceae), and crassinucellate ovules; the massive parietal tissue formed by both the primary parietal cell and the nucellar epidermis; multicelled archesporium and functioning of numerous megaspore mother cells; Polygonum type of female gametophyte; and multiple embryo sacs. Such features indicate that these are closely related and form a compact group. As shown by Sastri (1963), all these families also possess affinities with Lauraceae and perhaps with the Lauralian line of Eames (1961), and the theory that they might have had their origin from a common ancestry seems justified. Money *et al.* (1950) also included these families in their group having monocolpate or its derived forms of pollen grains, ethereal oil cells, and unilacunar nodes.

Lauraceae. The Lauraceae are relatively advanced over other Magnolian families, and Eames (1961) recognized two phylogenetic lines within the Ranales *sensu lato*, the magnolian line and the lauralian line, the latter including families such as Lauraceae, Hernandiaceae, Myristicaceae, Monimiaceae, and Gomortegaceae. Sastri (1963) has evaluated critically the morphological and embryological data and concluded that Hernandiaceae resembles Lauraceae in having unisexual flowers; stamens with 2-celled anthers and a glandular appendage with vascular supply; periplasmodial tapetum; successive type of cytokinesis; acolpate, 2-celled pollen; two-traced carpel; single anatropous ovule, and similar structure of the seed coat and pericarp; and that therefore, the two families are closely related (*see also* Shutts, 1960). Similarly Calycanthaceae are closely related to Lauraceae in having periplasmodial tapetum; multinucleate tape-

tal cells; anatropous, bitegmic, and crassinucellate ovules; multicelled archesporium; and Polygonum type of embryo sac. Pollen morphology (Erdtman, 1952) suggests close affinities with Hernandiaceae, Gomortegaceae, and Monimiaceae.

Sastri (1963) has rejected the possibility of any relationship with the Thymeleaceae since the latter family differs in having glandular tapetum with 4-nucleate tapetal cells; simultaneous cytokinesis; multiporate pollen; single-celled female archesporium; and both seed coats persistent. The resemblances, according to him, may be a case of parallelism.

Systematic position of *Cassytha*. Sastri (1962) has studied the embryology of *C. filiformis*, *C. glabella*, and *C. pubescens* and has found that the genus resembles most other Lauraceae in features such as type of cytokinesis; acolpate, 2-celled pollen; anatropous, bitegmic and crassinucellate ovules; multicellular female archesporium; Polygonum type of embryo sac; formation of seed coat by outer integument alone; and transformation of inner epidermis of pericarp into a stony layer. He (Sastri, 1963) concluded that its retention in the family Lauraceae is proper. However, there are also some important differences: (a) the tip of the nucellus is broad, so that the micropyle formed by the two integuments is very wide, (b) formation of multiple embryo sacs which are haustorial and start invading the nucellus at the 4-nucleate stage, 5 or 6 mature embryo sacs come out of the nucellus and invade even the overarching funicular tissue; (c) the antipodal cells are not organized and the three nuclei are ephemeral, (d) the endosperm is cellular in contrast to nuclear in rest of the family, (e) although the basic plan of seed structure is the same there are some differences in details. On the basis of such important dissimilarities as these, the present author considers that it would perhaps not be too unnatural to remove this genus to a separate family, the Cassythaceae, as proposed by Bartl. ex Lindley (1833) and recently adopted by A. C. Smith (personal communication). Certainly the two families are most closely related and probably derived from the same ancestral stock.

Cercidiphyllaceae and Trochodendraceae. *Cercidiphyllum* has been variously placed either in the Hamamelidaceae (Baillon, 1871; Croizat, 1947; Hallier, 1903; Lotsy, 1911; McLaughlin, 1933; Solereder, 1900), or in Magnoliaceae (Bessey, 1915; Diels, 1936; Hayata, 1921; Hutchinson, 1959; Lemesle, 1946), in Trochodendraceae (Harms, 1897), or in a separate family, the Cercidiphyllaceae (Cronquist, 1968; Harms, 1918; Takhtajan, 1966; Thorne, 1968). In all these treatments the relationships have been sought with other genera such as *Trochodendron*, *Tetracentron*, *Euptelea*, Hamamelidaceae, and members of the Magnoliaceae. Most recent taxonomists (Cronquist, 1968; Takhtajan, 1966; Thorne, 1968) keep Cercidiphyllaceae in the Hamamelidales. Such embryological features as single-layered glandular tapetum; absence of Ubisch granules; tricolpate pollen with conspicuously broad colpi; 1-celled female archesporium; nucellar cap formed by both the parietal cell and the nucellar epidermis; pattern of early growth of the endosperm. Con-

spicuous basal cell not taking part in the formation of embryo; ovules having vascularized tapering projection, and winged seeds in *Cercidiphyllum* indicate that the Cercidiphyllaceae are not related to the Magnoliaceae.

The chief evidences for including *Cercidiphyllum* either in Hamamelidaceae or in Cercidiphyllaceae placed close to Hamamelidaceae are the presence of stipules, palmate venation, marginal glands, tricolpate pollen, resemblances in wood anatomy to *Corylopsis*, and trilacunar node. The pollen although tricolpate differs basically. Further the resemblances in the wood anatomy may not indicate close relationships with certainty. The wings in the two families differ markedly in histological details (*see* Swamy & Bailey, 1949). Swamy and Bailey (1949) have taken into account the (i) idioblasts in the leaves, (ii) trends of specialization in the carpels, (iii) pollen grains, (iv) embryology, (v) seed structure, and (vi) wood characters, and they have concluded that the summation of evidence from all organs and parts clearly indicates that *Cercidiphyllum* cannot comfortably be included in any of the existing ranalian families. They agreed with van Tieghem (1900) that it should be placed in a separate family, the Cercidiphyllaceae. They remarked "Nothing is to be gained by transferring such genera as *Tetracentron*, *Trochodendron*, *Euptelea*, and *Cercidiphyllum* into close relationship with the Hamamelidaceae or Saxifragaceae, since this would merely serve to expand another order into a less homogeneous assemblage." To this conclusion I might add that the available evidences from embryology, morphology, anatomy, floral morphology, and cytology suggest that retention of this family within the Magnoliales would not make the order more heterogeneous than would its exclusion.

Trochodendron along with another primitive genus, *Tetracentron*, has been placed in the Magnoliaceae (Ranales), or in the Hamamelidaceae (Parietales). On the basis of vesselless xylem and primitive type of cambium in both these genera, Nast and Bailey (1945) supported the expulsion of the two genera from the family Hamamelidaceae, or Magnoliaceae and inclusion in separate families of their own, the Trochodendraceae and Tetracentraceae (*see also* van Tieghem, 1900). Embryology (Yoffe, 1962, 1965) supports this conclusion. Hutchinson (1959) includes *Euptelea* also in the Trochodendraceae. Nast and Bailey (1946), however, believe that *Euptelea* is rightly kept in a distinct family, the Eupteleaceae (cf. Lemesle, 1946).

Embryological information on Eupteleaceae and Tetracentraceae is lacking and any consideration of their interrelationship must await such data. Trochodendraceae and Cercidiphyllaceae resemble each other in having tricolpate pollen; anatropous, bitegmic, and crassinucellate ovules with a tapering chalazal projection; a circumscutous vascular bundle which enters the projection, then bends back to end at the base of the nucellus; a single-celled, hypodermal female archesporium; massive parietal tissue; the Polygonum type of embryo sac; cellular endosperm with a similar pattern in early development of endosperm; and a tapering wing

on the seed formed by the chalazal projection. Therefore, these families seem to be more closely related to each other than to any others in the Magnolian complex (*see also* Yoffe, 1965). On the basis of morphology and anatomy the Trochodendraceae are closely related to the Tetracentraceae (Bailey & Nast, 1945; Nast & Bailey, 1945; Smith, 1945).

Chloranthaceae. Various views have been expressed regarding the interrelationship of the Chloranthaceae, which have been considered related to Santalineae, Ceratophyllaceae, Piperales, or Ranales (*see* Bessey, 1915; Swamy, 1953; Hutchinson, 1959). Recently Takhtajan (1966) and Thorne (1968) have included the family in Laurales or Annonales respectively, whereas Cronquist (1968) retains this family in Piperales along with Saururaceae and Piperaceae. Vijayaraghavan (1964) has worked out the embryology of *Sarcandra irvingbaileyi* and evaluated its relationships with either Santalaceae or Piperaceae and Saururaceae. According to him (Vijayaraghavan, 1964) the summation of evidence fails to support any relationship with the families mentioned previously. The Chloranthaceae differ from Santalaceae in including autotrophic plants, with 2-celled pollen; superior ovary with 1 orthotropous bitegmic and crassinucellate ovule; a Polygonum type of embryo sac not developing beyond the ovule; and in lacking endosperm haustoria and having an Onagrad type of embryogeny. The family also differs from Saururaceae and Piperaceae in having unilacunar nodes; pollen with reticulate exine; tetrad of megaspores; and cellular endosperm. No close relationship seems to exist between them. The presence of monocolpate pollen, unilacunar node, and ethereal oil cells point towards ranalian affinities (*see also* Money *et al.*, 1950). Therefore, this family should be included in the Ranales *sensu lato* and the Magnoliales *sensu stricto*.

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POSTSCRIPT

Since this paper went to press one article was published on the morphology, embryology, and systematics of *Euptelea* (P. Endress, Gesichtspunkte zur systematischen Stellung der Eupteleaceen (Magnoliales). Ber. Schweiz. Bot. Ges. **79:** 229–278. 1969).

In *Euptelea polyandra* the anther wall is five- or six-layered (epidermis, fibrous endothecium, two or three middle layers, and glandular tapetum with one- to four-nucleate cells). After meiosis the microspore mother cells undergo simultaneous cytokinesis to produce tetrahedral tetrads. At the end of telophase I an evanescent cell plate appears in the equatorial plane. The pollen grains are shed at the two-celled stage. The carpel is peltate, stalked, without a style, and bears a stigmatic crest surrounding a ventral slit, thus resembling that of Schisandraceae, Winteraceae, and Degeneriaceae. The single ovule is pendulous, anatropous, bitegmic, and crassinucellate. Both integuments form the micropyle. The nucellar epidermis divides to form two- or three-layered tissue. The megaspore mother cell cuts off a parietal cell which produces massive tissue, the sporogenous cell becoming deeply buried in the nucellus. A linear tetrad of megaspores is formed, the chalazal one being functional and producing the Polygonum type of embryo sac. The synergids have a conspicuous filiform apparatus; the three uninucleate antipodal cells lie in a small tapering pouch. The endosperm is *ab initio* cellular; the first few divisions are transverse as in *Cercidiphyllum*. The embryogeny conforms to the Solanad type.

Endress (1969) concluded that, although *Euptelea* has its peculiar habit in common with *Eucommia ulmoides* and *Sycopsis sinensis*, evaluation of all other characters clearly indicates that it is most closely related to the Schisandraceae and *Cercidiphyllum* and belongs to the Magnoliales rather than the Hamamelidales.

The reader is also referred to the following recent papers:

SASTRI, R. L. N. Comparative morphology and phylogeny of the Ranales. Biol. Rev. **44**: 291–319. 1969.

SAMPSON, F. B. Studies on the Monimiaceae. I. Floral morphology and gametophyte development of *Hedycarya arborea* J. R. et G. Forst. (subfamily Monimioideae). Austral. Jour. Bot. **17**: 403–424. 1969a.

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CORRECTIONS

P. 6, l. 5, for *Pachylarnax phiocarpa* read *Pachylarnax pleiocarpa*.

P. 23, l. 14 from end, for *Laurelia novaezelandiae* read *Laurelia novae-zelandiae*.

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THE GENERA OF MYRICACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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MYRICACEAE Blume, Fl. Jav. Myric. 3. 1829, nom. cons.

(WAX-MYRTLE FAMILY)

Shrubs or small trees, usually aromatic and resinous, frequently of swampy, acid soils; branches terete, occasionally prostrate; roots fibrous, with numerous nitrogen-fixing nodules. Leaves with revolute vernation, alternate, simple, petiolate, entire, serrate to irregularly dentate, rarely pinnatifid, reticulately veined, generally with aromatic oil or resin glands, persistent or persisting until the next year's growth or deciduous, the leaf scars usually elevated, semiorbicular with three vascular trace scars; stipules usually absent, present only in *Comptonia* and there deciduous. Plants dioecious or occasionally monoecious. Flowers imperfect or rarely perfect, vernal, borne in usually dense unisexual aments, occasionally with aments androgynous or with functionally perfect proterogynous flowers. Staminate flowers subtended by a primary bract, the bract usually ovate to ovate-lanceolate and completely inclosing the stamens; perianth absent; stamens 2–8(–20), the filaments filiform, free or fused near the base; anthers dorsifixed, 2-locular, erect, introrse, with longitudinal dehiscence; pollen grains usually 3-porate, ± suboblate to subspheroidal. Carpellate flowers subtended by a usually ovate primary bract, secondary bracts present or absent, linear to lanceolate, usually 2 to 4, rarely more, the bracts persisting and elongating in fruit; perianth absent. Gynoecium bicarpellate, rarely tricarpellate, the ovary superior, 1-locular, the ovule solitary, basal, erect, orthotropous, with a single integument, style very short, divided into two, rarely three, stigmas which exceed the primary bract. Fruit drupaceous or nutlike, ± dry, often covered with variously

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References which I have not seen are marked by an asterisk.

I am grateful to Dr. Wood for his continuing help and editorial suggestions. Professor Ernst C. Abbe has kindly examined the illustrations and has offered valuable suggestions concerning the interpretation of the inflorescences found in the Myricaceae. The illustrations, the work of Miss Virginia Savage, were prepared from materials collected by R. J. Eaton, N. G. Miller, C. E. Wood, Jr., and the author. Mrs. Nancy Dunkly has helped greatly with the preparation of the manuscript.

shaped protuberances, smooth, lustrous to glandular, frequently with a waxlike coating, inclosed or not by persistent bracts. Seed erect; seed coat thin; endosperm a single layer of cells; embryo straight, the cotyledons ± fleshy, plano-convex, the radicle superior, short. Base chromosome number 8. (Galeaceae Bubani.) TYPE GENUS: *Myrica* L.

A small family of one, two, or three genera including approximately 40 to 50 species, mainly in mild-temperate to subtropical regions of the world, including southern Africa. The number of genera comprising the Myricaceae remains in question. If *Myrica* is treated in the broad sense, the family consists only of the one genus (Gray, Lessons Man. Bot., 1887; Engler, Nat. Pflanzenfam. III. 1: 27. 1894; Rendle, 1925). Some workers (Rehder, Man. Cult. Trees Shrubs, ed. 2. 1940; Bailey, Man. Cult. Pl., 1949; Fernald, Gray's Man. Bot. ed. 8. 1950; Melchior, 1964; Hutchinson, 1967) have preferred to recognize the monotypic genus *Comptonia* as distinct from *Myrica*, mainly because of the presence of stipules and of secondary bracts that elongate and persist in the nutlike fruit. Still other workers (e.g., Chevalier, 1901; Radford, Ahles & Bell, Man. Vasc. Fl. Carolinas, 1968) have preferred to recognize the two subgenera of *Myrica* as distinct genera. The difficulty of generic delimitation within the family is not in the recognition of the three taxa but in the rank to be assigned to each. The poorly known *Canacomyrica* Guill. is attributed to the Myricaceae but differs in having a pendulous ovule and bifid stigmas, characters which suggest that it belongs to another family.

Members of the Myricaceae are shrubs or small trees with fragrant, often glandular-dotted leaves, and generally with unisexual aments and a one-locular ovary with a single, erect, orthotropous ovule. The monotypic *Comptonia* and *Myrica*, with four species of subg. *Morella* and a single species of subg. *Myrica*, occur in our range. Two species of *Myrica* (one of each subgenus) are restricted to the Pacific Coast of the United States. Several species described from Central America and the West Indies warrant further study, since some may ultimately prove to be conspecific with those of the United States.

The Myricaceae are presently considered by most workers to be the only family of the order Myricales, although Hjelmqvist (1948) placed the family in the Juglandales. The order Myricales is characterized by the unilocular ovary, the single orthotropous ovule, and the short style with two stigmas. On the basis of vegetative, floral, and fruiting similarities the Myricales are most closely allied with the Garryales and Leitneriales. Cronquist (1968), however, places the Myricales peripheral to the Fagales and Juglandales, while Takhtajan (1969) considers the Myricales to have much in common with the Casuarinales and Betulaceae as well as with the Juglandales.

Initial studies of the staminate inflorescences in the Myricaceae by E. C. Abbe have shown them to be panicles (*Myrica*) or by reduction a lax primary axis bearing primary bracts with four or fewer stamens in the axils (*Comptonia*, *M. Gale*). The most complex panicles are found

in *M. javanica* Blume, of Asia, while New World species have more reduced panicles indicative of their greater specialization. A progressive reduction was observed in the complexity of branching and in an often accompanying reduction in the number of bracts and stamens. Concomitant studies of the xylem anatomy of the Myricaceae by L. B. Abbe confirmed the advanced status of *Comptonia* within the family. In *Comptonia* the single-pore condition in a large number of the secondary vessel elements contrasts with the less specialized many-perforate end walls of those of *M. Gale*.

The Myricaceae is an old family with a fossil record from the Upper Cretaceous to the present. Members of this family apparently were much more numerous and widespread than the distribution of the extant species indicates. During the Tertiary the Myricaceae were apparently more abundant in Europe than in the United States.

Of little primary economic importance, the Myricaceae because of their relative abundance in swampy areas serve as a food source for certain wildlife. Most members of the family have nitrogen-fixing root nodules that not only enrich the soil in which they are growing, but give them a competitive advantage over other plants in areas low in combined nitrogen.

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KEY TO THE GENERA OF MYRICACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Shrubs or trees, dioecious or occasionally monoecious; leaves simple, usually lacking stipules, often resinous dotted and fragrant; aments usually unisexual; flowers bracteate; fruit drupaceous or nutlike, frequently with a waxlike coating.*

Leaves entire, dentate, serrate or slightly incised, lacking stipules; fruits with or without a waxlike covering or resinous dotted, bracts 2 to 4, not longer than the fruit or absent. . . . . 1. *Myrica.*

Leaves pinnatifid, with semicordate stipules; fruits glabrous, nutlike, bracts 6 to 8, linear-subulate, persistent, longer than the fruit. . . . . 2. *Comptonia.*

1. **Myrica** Linnaeus, Sp. Pl. 2: 1024. 1753; Gen. Pl. ed. 5. 449. 1754.

Shrubs or small trees of dry or swampy areas; branches terete, usually glandular dotted, slender, the lower ones occasionally prostrate; buds small, scaly. Leaves persisting until the following year's growth or deciduous, entire, serrate, sparingly dentate near the apex [pinnately lobed], glandular dotted, aromatic when crushed, membranaceous to coriaceous; stipules lacking. Plants usually dioecious, infrequently monoecious. Flowers usually imperfect, borne in aments. Staminate aments ellipsoid to cylindric, more or less erect, sometimes appearing spikelike; flowers solitary in the axils of bracts, the primary bract generally ovate; stamens 2–20; filaments free or often united near the base; rudimentary gynoecium occasionally present. Carpellate flowers in ovoid to cylindric,

sometimes interrupted aments; stigmas two, exceeding the ovate primary bract; style short; ovary sessile, subtended by 2 to 4 secondary bracts, these sometimes absent, persisting and enlarging in fruit in *M. Gale*. Fruit drupaceous, ± dry, globose to ovoid, often covered with variously shaped protuberances, usually with a waxy coating that becomes white in drying, infrequently glandular dotted. (*Gale* Duham., nom. superfluum; *Morella* Lour.; *Faya* Webb & Berthel.). LECTOTYPE SPECIES: *M. Gale* L.[2]; see Britton, N. Am. Trees, 209. 1908; Britton & Brown, Illus. Fl. No. U.S. ed. 2. 1: 584. 1913; Abrams, Illus. Fl. Pacific States 1: 508. 1923; Hitchcock & Green, Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 191. 1929. (Name Latin, adopted from Greek *myrike*, the name of tamarisk.) — WAX MYRTLE, BAYBERRY, SWEET GALE.

Subgenus MORELLA (Lour.) Engler (*Cerophora* Raf.; *Fayana* Raf.; *Faya* Webb & Berthel.; *Cerothamnus* Tidestrom; *Myrica* sect. *Morella* (Lour.) Benth. & Hooker; *Myrica* sect. *Cerophora* (Raf.) Chevalier), with perhaps 25 to 30 species distributed mainly in temperate regions of the world but also extending into Latin America and Africa, is represented in our area by four species in two sections. Plants in this subgenus have the aments borne on old wood, mainly below the leaves; the bracts of the staminate flowers are shorter than the stamens; and the ovary and fruit are globose at maturity with numerous protuberances which usually have heavy waxy coating that frequently dries white. In his revision of the Myricaceae, Chevalier divided *Myrica, sensu* Chev., into sect. MORELLA, of eastern and southern Asia and the Malayan Archipelago; sect. FAYA, of western and southern coastal United States and the Canary Islands, Madeira, and the Açores; and sect. CEROPHORA, of Africa and temperate to tropical America. Four species of subg. MORELLA are found in our range: *M. inodora* of sect. FAYA and *M. pensylvanica*, *M. cerifera*, and *M. heterophylla* of sect. CEROPHORA.

Section CEROPHORA,[3] distinguished by simple catkins, spikelets reduced to a single flower, solitary or in threes in the axil of a bract, and fruits 1–5 mm. in diameter, usually with a waxy covering and not fleshy, consists of 25–30 species of both the Old and New Worlds. Found mainly near the coast or on the Coastal Plain, *Myrica pensylvanica* Loisel., $2n = 16$, northern bayberry, is distributed from Newfoundland and Nova Scotia south to North Carolina and locally to Ohio. A low shrub or small tree, this species is distinguished by whitish-gray or drab branches; deciduous to subpersistent, membranaceous, elliptic, oblanceolate or obovate leaves, mostly lacking resin glands on the upper surface; and dense-

[2] Most authors have followed the selection of *M. Gale* as the lectotype of *Myrica*, although Hylander (1945) designated *M. cerifera* L. as the lectotype in place of *M. Gale*, on the mistaken assumption that *Gale* Duhamel (attributed by Chevalier, 1901, to Adanson) was a legitimate name and that *M. Gale* had thus been removed from *Myrica*.

[3] Chevalier divided sect. CEROPHORA into two subsectional categories, Americanae and Africanae, but without indication of rank, and they apparently have not been assigned one by a subsequent author (cf. ICBN, 1966, Art. 35).

FIGURE 1. **Myrica** subg. **Morella.** a–f, *M. pensylvanica*: a, branchlet with staminate inflorescences, × 1; b, staminate flower, × 10; c, staminate flower, lateral view, showing filaments, × 10; d, carpellate inflorescence, × 6; e, carpellate flower with bracts, × 15; f, semidiagrammatic longitudinal section of carpellate flower to show ovule, × 20. g–i, *M. cerifera*: g, fruiting branchlet, × 1/2; h, fruit, × 8; i, semidiagrammatic longitudinal section of fruit, showing endocarp and embryo, × 8.

ly pubescent young fruits. It reportedly hybridizes with *M. cerifera* to produce *M.* × *Macfarlanei* Youngken.

A large shrub or small tree, *Myrica heterophylla* Raf., myrtle, evergreen bayberry, or wax myrtle, occurs along the Coastal Plain in thickets and woods from southern New Jersey to Florida and west to Louisiana. The features used to identify this species include its blackish branches; pilose leafy branchlets; coriaceous, evergreen, elliptic to obovate leaves; and glabrous young fruits. On the basis of its nearly glabrous branchlets Fernald (1938) recognized var. *Curtissii* (Chev.) Fern. (*M. Curtissii* Chev.), but later workers (Little, 1953) have not accepted it as distinct. Gleason & Cronquist (Man. Vasc. Pl., 1963) question the recognition of this taxon and suggest that it may be a hybrid of *M. pensylvanica* and *M. cerifera*, a hypothesis that should be investigated.

The southern bayberry, *Myrica cerifera* L. (*Morella cerifera* (L.) Small, *Cerothamnus ceriferus* (L.) Small, *Myrica carolinensis* Mill., *C.*

carolinensis (Mill.) Tidestrom), $2n = 16$, occurs in swampy or sandy soils in low, acid prairies, thickets and woods, principally along the Coastal Plain from southern New Jersey to southern Florida, west to eastern Texas and southeastern Oklahoma, and north to Arkansas. It also occurs in Bermuda, the Greater Antilles, Mexico, and Central America. Taxonomically important characters are the heavily resinous-glandular glabrescent branchlets; narrowly oblanceolate, coriaceous, persistent leaves, abundantly resinous-glandular on the upper surface; and glabrous fruit. The fruit is eaten by numerous coastal birds, including quail and apparently wild turkey in some areas.

Although *Myrica pusilla* Raf. (*Cerothamnus pumilus* (Michx.) Small), $2n = 16$, was recognized as a distinct species by both Fernald (Gray's Man. Bot. ed. 8, 1950) and Gleason (New Britton & Brown Illus. Fl. Northeast. U.S. Vol. 2. 1963), Radford, Ahles, & Bell (Man. Vasc. Fl. Carolinas, 1967) treated it as *M. cerifera* var. *pumila* Michx. It appears that *M. pusilla* is merely a smaller xeric form of *M. cerifera* that does not merit specific status (Thieret, 1966). Varietas *pumila* occurs on dry, sandy pinelands and prairies from eastern Texas and Louisiana, east to Florida and north to North Carolina. The status of this questionable variety should be investigated more thoroughly.

Section Faya, characterized by simple or branched aments, carpellate spikelets with several flowers, of which only some develop, and fruits 4–6 mm. in diameter, includes only three species. *Myrica inodora* Bartr. occurs in our range; *M. californica* Cham. occurs only along the west coast of the United States from Washington south to California; and *M. Faya* Ait. is restricted to Madeira, the Canary Islands, the Açores, and Portugal (where it is naturalized or possibly indigenous). This type of distribution of closely related species is further evidence of the relict nature of the genus.

Lacking the almost characteristic myricaceous scent, *Myrica inodora* Bartr. (*Morella inodora* (Bartr.) Small; *Cerothamnus inodorus* (Bartr.) Small), odorless bayberry, occurs sparingly in the Gulf Coast pineland swamps from southeastern Louisiana to northwestern Florida. This evergreen shrub is recognized by its smooth, reddish-brown branchlets that are scurfy tomentose when young but later pubescent to glabrous; by its oblong-obovate to ovate coriaceous more or less glandular leaves with the margin usually entire, rarely with a few serrations apically; and by its glabrous fruit.

Subgenus Myrica (subg. *Gale* [Duham.] Engler; *Gale* Duham.; *Cerophora* subg. *Galestis* Raf.; *Angeia* Tidestrom) includes *M. Gale* L. (*Gale palustris* (Lam.) Chev.), $2n = 48$, ca. 96, sweet gale, of northwestern Europe, northern North America, and northeastern Asia, and *M. Hartwegii* S. Wats., of the Sierra Nevada in California. Found principally in swampy areas, *M. Gale* is distributed in North America from Labrador to Alaska, south to Newfoundland, Long Island and Pennsylvania, west to Michigan, Minnesota, Wisconsin, and Washington and Oregon. It reaches our range in Tennessee and in bogs, now largely drained, in Henderson

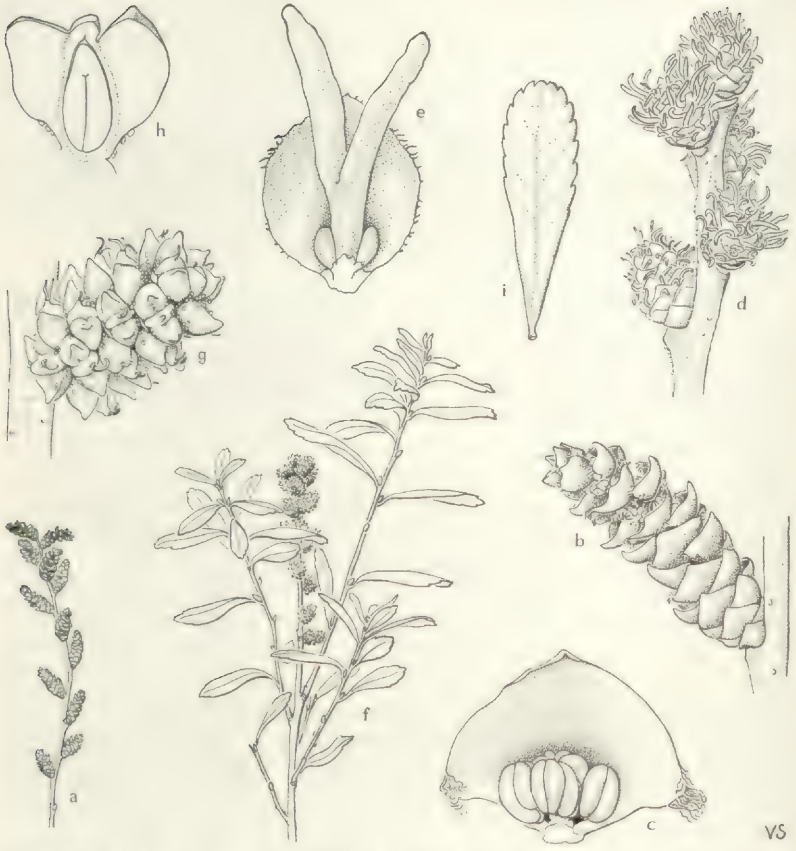

FIGURE 2. **Myrica** subg. **Myrica**. *M. Gale*: a, branchlet with staminate inflorescences, × 1/2; b, staminate inflorescence, × 3; c, staminate flower with bract, × 10; d, branchlet with carpellate inflorescences, × 4; e, carpellate flower with bract and two lateral secondary bracts, × 25; f, habit with mature fruits, × 1/2; g, mature fruits of a single carpellate inflorescence, × 4; h, semidiagrammatic longitudinal section of fruit, showing fleshy secondary bracts and embryo, × 12.

County, North Carolina. The species, as well as the subgenus, is characterized by aments borne near the summit of the branchlets of the preceding year; by the bract of the staminate flower longer than the stamens; by the smooth fruit each flanked by two accrescent, more or less fleshy secondary bracts; and by the lack of a heavy wax deposit on the surface of the fruits. The considerable variation in the amount of pubescence has led to the recognition of var. *subglabra* (Chev.) Fern. in eastern and var. *tomentosa* C. DC. in Pacific North America and Eurasia.

The few chromosome counts suggest that European populations of *M. Gale* are hexaploids ($2n = 48$), while those from western North America

are apparently dodecaploids ($2n$ = ca. 96 in plants from the Queen Charlotte Islands). Further counts are needed throughout the range of the species to determine the extent and levels of polyploidy and its significance.

An interesting phenomenon in *M. Gale* is the great plasticity in the sexes of individual flowers as well as individual plants. Three types of monoecious plants occur (Davy & Gibson, 1917): both staminate and separate carpellate aments may occur on the branchlets of a single plant; the branchlets may produce androgynous aments with staminate flowers on the lower part of the ament; or in some aments perfect proterogynous flowers capable of producing fruit can be found. In addition, the sex of a plant of *M. Gale* may vary from one year to the next, from undetermined causes.

Most, if not all, species of *Myrica* have numerous nodules on the roots, including the adventitious ones arising from prostrate stems or rhizomes. Recent investigations by Bond have clearly demonstrated that the nodules, especially those of *M. Gale*, are accumulators of nitrogen. Bond (1958) postulated that the nitrogen fixing nodules of *Myrica* species may have been the original and principal source of symbiotic nitrogen in temperate regions following the Pleistocene.

Known best to the nonbotanist for their role in candle making, *Myrica cerifera*, *M. pensylvanica*, *M. heterophylla*, and to a lesser extent, *M. inodora* were sought by early settlers of the eastern United States. The fruits were gathered in the fall and placed in boiling water, the waxlike coating (a fat composed mainly of palmitin or palmitic acid) then melting and rising to the surface was skimmed off for use in candle making. Today most bayberry candle fat is imported into the United States from South America. In the eastern United States the making of bayberry candles with locally gathered fat has become a novelty or tourist attraction. In Europe bayberry fat is used in the manufacture of soap, probably for its pleasant scent.

Of limited economic importance, the buds and mainly the fruits serve as a food source for wildlife, especially birds. Muskrats have been observed feeding upon the fruits of *M. Gale*, and the buds and aments are eaten by sharp-tailed deer. The bark of *Myrica cerifera* and *M. pensylvanica* were once used in moderate amounts as an astringent and in larger amounts as an emetic. The bark in the form of a powder or in a decoction was also used to treat inflammations, ulcers, and many other internal problems. It has been reported that the leaves can be used as a substitute for bay leaves (*Laurus nobilis* L.) in flavoring stews and soups. Because of their habit of growth various species are effective in controlling erosion. Several species are attractive ornamental shrubs in cultivation.

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2. Comptonia L'Heritier ex W. Aiton, Hort. Kew. 3: 334. 1789.

Low-growing shrubs; branches terete, brown, villous to minutely puberulent, fragrant. Leaves appearing after flowering, pinnatifid with rounded lobes, membranaceous, linear-lanceolate, deciduous or persisting until the following spring, glabrous to densely pubescent, short-petiolate; stipules present, semicordate becoming subfoliaceous, deciduous. Plants monoecious or dioecious; flowers usually imperfect, borne in axillary aments. Staminate flowers in cylindrical, flexuous aments near the apex of the branchlets; primary bract cordate, reniform; stamens 3–8; filaments free. Carpellate flowers generally in erect globose-ovoid aments,

FIGURE 3. **Comptonia.** *C. peregrina*: a, branchlet with staminate inflorescences, × 1/2; b, staminate inflorescence, × 3; c, bract of staminate flower, × 12; d, staminate flower with bract, × 12; e, lateral view of staminate flower in partial section, × 12; f, carpellate inflorescence, × 6; g, carpellate flower at time of pollination, × 25; h, carpellate flower following fertilization showing development of primary bracts, × 12; i, carpellate flower after fertilization showing development of both primary and secondary bracts, × 12; j, young fruit with semipersistent styles, × 6; k, branchlet with mature fruit and accessory bracts, × 1; l, mature fruit, × 6; m, semidiagrammatic longitudinal section of mature fruit to show embryo, × 6; n, mature leaf, × 1.

usually on older wood, the primary bract usually ovate, pubescent, at least near the base; each flower subtended by 6–8 minute linear to acicular secondary bracts that persist and elongate in fruit (see FIGURE 3, g–i, k). Fruit a small ovoid-oblong, smooth, shining nut. TYPE SPECIES: *C. asplenifolia* (L.) L'Her. ex W. Ait. = *C. peregrina* (L.) Coult. (Name commemorating H. Compton, 1632–1713, an amateur horticulturist and supporter of botany, who also served as Bishop of London.) — SWEET FERN.

A single extant species, *Comptonia peregrina* (L.) Coult., $2n = 32$, sweet fern, found on poor, often rather dry soils in woodlands, clearings, pastures, and pine barrens from Nova Scotia to Saskatchewan, south to Virginia, western North Carolina (but also in four counties in the lower Piedmont), extreme western South Carolina, and locally in northern Georgia and Tennessee, Ohio, northwestern Indiana, Illinois and Minnesota. The rather attractive low shrub with its fragrant aroma when crushed has been separated into two varieties. The questionably distinct var. *asplenifolia* (L.) Fern., of the Coastal Plain pinelands or pine barrens from Long Island, New York, to Virginia, is characterized by the minutely puberulent branchlets, sparsely short-puberulent or glabrous leaves, and fruits 3–4 mm. long. The more northern and inland var. *peregrina* has more or less pilose branchlets, pilose leaves, and fruits 4–5 mm. long.

The six to eight secondary bracts associated with a single pistillate flower suggest that the solitary flower is derived by reduction from a few-flowered cyme. The inner secondary bracts would be the only grossly observable remnants of the cyme. A second possibility is that the inner secondary bracts are actually modified perianth parts that are completely lacking in *Myrica*. A careful anatomical study of the flowers and aments is needed.

Comptonia peregrina is the only survivor of a genus that had perhaps a dozen species in the Eocene and Oligocene. Berry (1906) postulated that *Comptonia* developed in the Upper Cretaceous as a branch from *Myrica* stock, but supporting evidence is lacking. Numerous Tertiary fossils of *Comptonia* clearly demonstrate that several species once occupied regions throughout much of the temperate world. In European Tertiary deposits, *C. difformis* (Sternh.) Berry is the most common fossil species of the genus (Kotlaba, 1967).

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COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, VII. ADDITIONAL NOTES ON ACROTREMA

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I HAVE POINTED OUT during this series of papers that the Dilleniaceae is comprised of genera possessing considerable morphological diversity, a result in part of the wide range of growth habits encountered. One of the most interesting, yet least studied genera in the family, is *Acrotrema* Jack, a rhizomatous, semi-herbaceous plant.

Acrotrema is of interest not only because it is a small, nearly herbaceous plant in an otherwise woody family (the Australian genus *Pachynema* is also for the most part non-woody), but its constituent species show a remarkable degree of morphological variation (see FIGURES 35–43). From an evolutionary viewpoint, the genus is noteworthy because it is one of the few dicotyledonous herbs in which the vessel elements possess exclusively scalariform perforations (Takhtajan, 1954, p. 119). Furthermore, Meeuse (1966, p. 204) suggests that, "the pinnate or bipinnate leaves of the acaulescent Acrotremeae are also suggestive of a fern-frond, i.e., a pteridospermous-cycadopsid phyllome, and one of the possible habit forms of the 'reconstructed' group of Protodicots."

The genus has been generally considered to consist of about ten species and a number of varieties, all of which are confined to Ceylon with the exception of *A. costatum* Jack from Thailand and the Malay peninsula, and *A. arnottianum* Wight from southern India. Indications are that some of the species are very narrowly endemic and apparently quite rare.

The only comprehensive taxonomic treatments available are those prepared by G. H. K. Thwaites (1864) in his *Enumeratio plantarum Zeylaniae: An Enumeration of Ceylon Plants* . . ., by Hooker and Thomson (1872) for J. D. Hooker's *The Flora of British India*, in which they comment that *Acrotrema* is, "A remarkable genus of very variable species," and by H. Trimen (1893) for his *A Hand-Book to the Flora of Ceylon*. Trimen commented, "Most of the species are ill-defined and extremely variable, and I have failed to obtain any clear idea of their limits. They doubtless hybridise freely." Anatomical information is meager and accurate illustrations do not exist.

I recently had the good fortune to secure an excellent assemblage of well-preserved specimens of *Acrotrema* resulting from the collecting efforts of Dr. R. D. Hoogland of the Australian National University. The assistance Dr. Hoogland has given me now and in the past is acknowledged with much appreciation. Although many of these collections are currently without names, they are all vouchered and are being studied in

connection with a new generic treatment for a proposed flora of Ceylon.

The present paper draws attention to this uncommon and little-known dilleniaceous genus and provides additional morphological information, including the report of new anatomical features for the family.

MATERIALS AND METHODS

Liquid-preserved vegetative and floral material was received from Dr. R. D. Hoogland. Hoogland collection numbers *11423*, *11460*, *11469*, *11572*, *11575*, *11580*, and *11583* were collected in Ceylon and have voucher specimens housed at the Commonwealth Scientific and Industrial Research Organization, Division of Plant Industry, Canberra, Australia (CANB); Department of Agriculture, Peradeniya, Ceylon (PDA); and the United States National Museum, Washington, D.C. (US). The Hoogland collection of *Acrotrema costatum* (*11635*) was obtained in Penang, Malaya, and has supporting material in CANB. Additional preserved plants of *A. costatum* were received through the efforts of Mr. K. C. Chiang at the Botanic Gardens, Penang. The following specimens of *Acrotrema* at the United States National Museum were also examined; these for the most part are very old sheets with Thwaites collecting numbers:

Acrotrema sp. **Ceylon:** *Thwaites* C.P. *3898*; *A. appendiculatum* Thw. **Ceylon:** *Thwaites* C.P. *3880*; *A. bullatum* Thw. **Ceylon:** *Thwaites* C.P. *239*; *A. costatum* Jack. **Thailand:** *Smitinand 2999*; *A. dissectum* Thw. **Ceylon:** *Thwaites* C.P. *3393*; *A. Gardneri* Thw. **Ceylon:** *Thwaites* C.P. *253*; *A. lanceolatum* Hook. **Ceylon:** *Thwaites* C.P. *2660*; *A. rugatum* Thw. **Ceylon:** *Thwaites* C.P. *3899*; *A. Thwaitesii* Hook. **Ceylon:** *Thwaites* C.P. *3364*; *Thwaites* C.P. *3969*; *A. uniflorum* Hook. **Ceylon:** *Thwaites* C.P. *3486*; *A. Walkeri* Wight. **Ceylon:** *Thwaites* C.P. *694*. Material of *A. arnottianum* was not available for study.

Histological details were revealed primarily through the use of paraffin-embedded and sectioned material subsequently stained with safranin-fast green or lacmoid. Several flowers and leaves were also cleared with 5% NaOH to study vasculation. Epidermal features were examined by making peels from preserved leaves. Pollen was acetylized and mounted in glycerine jelly.

The assistance of Miss Marion Seiler, staff artist in the Department of Botany, The University of North Carolina, Chapel Hill, is sincerely appreciated.

GENERAL MORPHOLOGY

The genus *Acrotrema* is composed of perennial herbs with simple leaves. Surprisingly, Hoogland (personal communication) mentions collecting specimens which were epiphytic. FIGURES 35–43 illustrate some of the variability in lamina dissection. FIGURES 35, 36, 37, and 38 represent plants with leaves that are undivided and generally obovate-oblong. The

leaves of *Acrotrema gardneri* (FIGURE 39) are narrowly oblong to linear-spathulate whereas those of *A. lanceolatum* (FIGURE 40) are characteristically linear-lanceolate in outline. The margins are entire, serrate, or dentate. FIGURES 41 and 42 show specimens of *A. Thwaitesii* with linear-lanceolate, pinnatifid leaves. The most dissected situation occurs in *A. dissectum* (FIGURE 43) in which the leaves are bipinnate with the largest segments deeply cleft and one or more pairs of small segments situated between the large ones. *Acrotrema lyratum* (not pictured) is described as having lyrately lobed leaves with four to five pairs of basal lobes, and *A. arnottianum* has been pictured as possessing large, entire leaves (Swamy & Periasamy, 1955). A study of the stability of leaf morphology in this genus in addition to chromosome data would be of interest. Thwaites's collection of *A. appendiculatum* Thw. (C.P. *3880*) is distinguished by the presence of rows of large, circular cushions between the secondary veins of the leaf (FIGURE 37). The foliage of *A. costatum* and many of the Ceylonese plants is variegated along the midrib as shown in FIGURE 20. The petioles sheath the stem and possess membranous, caducous wings. Young leaves exhibit conduplicate vernation (FIGURE 29) as is characteristic of other Dilleniaceae.

The stem is typically very short and in some cases the plants appear acaulescent. *Acrotrema costatum* (FIGURE 20) has a comparatively elongated axis which is readily divided into a pubescent aërial segment bearing crowded leaves and leaf scars, and an underground rhizomatous portion. With the exception of the primary root, all roots are adventitious. The endogenous origin of the roots from the stem has been illustrated in *Plate I, Figure 4* of Dickison (1969).

The inflorescence is a terminal or axillary raceme, occasionally reduced to a single flower. Each flower is subtended by a membranous bract. The length of the peduncle and degree of pubescence has been used to separate species. On the basis of general floral morphology, *A. costatum* from Malaya (FIGURES 9–15) is clearly distinguishable from most species inhabiting Ceylon (FIGURES 1–8). In the latter, the androecium is externally fasciculate with three stamen fascicles alternating with three carpels (*A. Thwaitesii* is an exception). Individual stamens possess long filaments and short anthers which open by longitudinal slits (FIGURES 6, 8). The androecium of *A. costatum* does not show external fasciculation but rather the fifteen stamens arise from the receptacle uniformly around the carpels. Stamens have elongated microsporangia which dehisce by apical pores (FIGURE 12). The gynoecium is usually described as consisting of three basally connate carpels; however, I have examined racemes in which some or all of the flowers were bicarpellate (FIGURE 11). The morphology of the carpels agrees essentially with previous descriptions (Dickison, 1968). Carpels are glabrous and differentiated into a swollen ovary and slender, sometimes recurved, style terminated by an indistinct stigmatic surface. The two or three conduplicate carpels are laterally concrescent (FIGURES 25, 26). At the level of placentation the ventral suture opens to produce a central cavity. Progressing distally, the

carpels close and become totally apocarpous at the initiation of the stylar region. The bicarpellate gynoecium of *A. costatum* has an opposite orientation as interpreted by Wilson (1965). The ovules are arranged in two rows along the placenta and range in number from two to many. Raphides are a characteristic feature in the carpel wall. The fruit is a follicle and the seeds are arillate. The flowers have five pubescent sepals and five glabrous petals which contain numerous raphides.

VEGETATIVE ANATOMY

Trichomes. The trichome complement of *Acrotrema* is unusually diverse and includes types previously unknown for the family. A dense pubescence may cover the aërial stem (FIGURE 20) and also young floral buds, pedicels and peduncles (FIGURES 1, 9, 10). On the leaf, hairs are conspicuously abundant along the major veins of the abaxial surface and margins of the lamina. Foliar trichomes are not uniform in length but are noticeably longer along the veins than in intercostal regions.

Compared to other Dilleniaceae, the prevalent trichome type is a unicellular, unbranched form. Frequently, however, these hairs are raised on pedestals of enlarged cushion cells (FIGURE 24), a feature not typical among other members of the family. A few septate hairs with varying numbers of cells and their outer walls divided into two layers were observed (FIGURE 23).

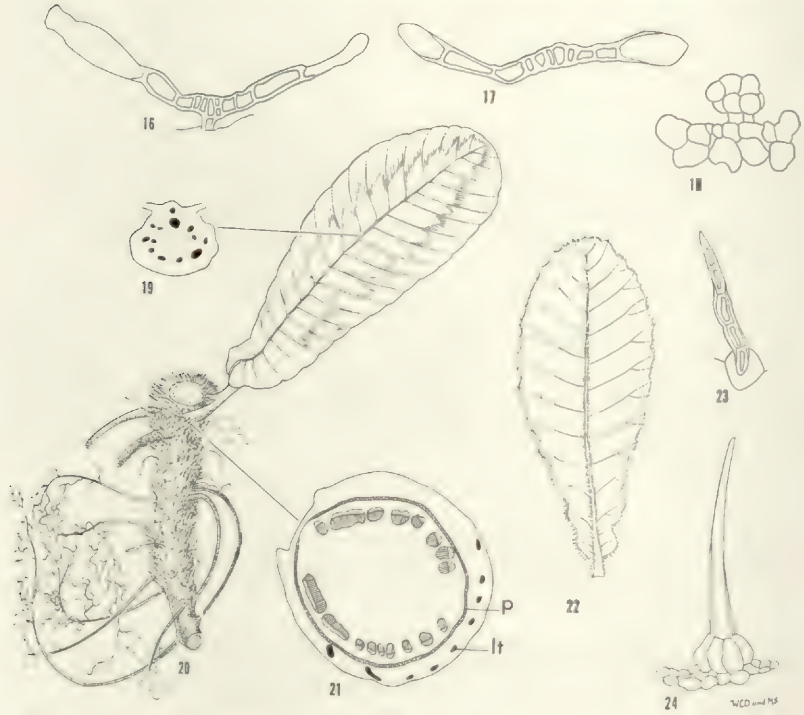
Acrotrema also possesses glandular trichomes. Glandular hairs are very abundant on sepals and to a lesser degree on the leaves. One type of glandular hair consists of a multicellular stalk and globose head (FIGURE 18), the contents of which stain very darkly. Another form observed on the leaves of *A. costatum* is composed of a cluster of swollen cells situated in depressions on the lower surface of the lamina (FIGURE 34). A third category of glandular trichome, which is very abundant on sepals and pedicels of *A. costatum*, is the most complex and diagnostic in the entire family. As seen in FIGURES 16 and 17, these trichomes are basically two-armed with a short stalk and spreading, multicellular arms that terminate with a much enlarged, clavate, thin-walled cell. This trichome is exceptional for the family and has surprisingly been overlooked in previous descriptions of the genus.

Leaf. Dorsiventral. Hairs of the type described above. Epidermis is composed of uniformly thickened, thin-walled cells. Cells of the abaxial epidermis tend to be isodiametric with straight walls whereas those of the adaxial surface are noticeably more sinuous. Costal cells are elongated and trichomes are surrounded by specialized "accessory cells." Stomata are abundant and confined to the abaxial surface (FIGURE 31). Mature stomata are anisocytic (*sensu* Metcalfe and Chalk, 1950), i.e., three subsidiary cells of which one is smaller than the other two, surround the stoma (FIGURE 33). This is the first report of the anisocytic stomatal pattern in the Dilleniaceae. Guard cells have an average length of 26 μ

FIGURES 1–15. Floral morphology of *Acrotrema*. 1–8. *Acrotrema* sp. (from *Hoogland 11469*, Ceylon). 1, Lateral view of open flower, × 2; 2, open flower seen obliquely from above, × 3; 3, flower seen obliquely from beneath, × 2; 4, gynoecium of 3 carpels, × 3.5; 5, petal, × 3; 6, stamen, × 6; 7, sepal, × 3; 8, anther, showing longitudinal dehiscence, × 6. 9–15. *A. costatum* (from *Hoogland 11635*). 9, Oblique view of flower from above, × 2; 10, same, from beneath, × 2; 11, lateral view of bicarpellate gynoecium, × 3.5; 12, front view of stamen, × 4; 13, same, from side, × 4; 14, sepal, × 3; 15, petal, × 3.

and contain numerous chloroplasts. The mesophyll is differentiated into palisade and spongy layers although they are not sharply defined (FIGURE 31). A weakly differentiated hypodermis is evident in *A. costatum*. Raphides are common. Subepidermal layers of collenchyma occur around the midrib. I have drawn attention elsewhere (Dickison, 1969) to the marked differences in petiole vasculation between *A. costatum* and the

Ceylonese species, where initially three bundles give rise to an abaxial arc of vascular tissue and an adaxial bundle. The petiole of *A. costatum* is supplied by a large number of traces (ca. 9) which divide in the midrib to become orientated as thirteen widely separated collateral bundles (FIGURE 19). The larger bundles have outer sclerenchymatous caps. A large central bundle is located adaxially, above which a conspicuously smaller bundle occurs with inverted vascular tissue. In species with undissected leaves, the vasculation of the lamina is pinnate with strong secondary veins terminating at the margins (FIGURE 20). Many species from Ceylon have secondary veins which fork noticeably at the margins (FIGURE 22), not a common feature among other dilleniaceous genera.



FIGURES 16–24. Vegetative morphology of *Acrotrema*. 16, Lateral view of glandular trichome from sepal of *A. costatum* (*Hoogland 11635*), × 62; 17, same, seen from above, × 62; 18, glandular trichome from sepal of *Acrotrema* sp. (*Hoogland 11423*), × 62; 19, transverse section through midrib of leaf of *A. costatum* (from Penang, Malaya, *s.n.*) showing widely separated vascular bundles, × 4; 20, habit of *A. costatum* (from same coll.), × 1/2; 21, transverse section through stem at nodal level showing departing leaf traces (lt), initiation of periderm (p), and eustele composed of collateral bundles, × 4; 22, leaf of *A. walkeri* (*Thwaites* C.P. *694*), showing pubescence and pinnate venation, × 1/2; 23, multicellular, unbranched trichome from the sepal of *Acrotrema* sp. (*Hoogland 11423*), × 62; 24, unicellular trichome elevated on pedestal, from sepal of *A. costatum* (*Hoogland 11635*), × 62.

Stem. The stem is circular in outline in transverse section. The aërial portion of the stem is densely pubescent in *A. costatum* and other species. The epidermis is thin-walled and not distinct from underlying cortical cells. The cortex is wide and uniformly parenchymatous as is the pith. An endodermis is lacking. Scattered throughout the parenchymatous regions of the stem are mucilaginous raphide-containing idioblasts and in *A. costatum* starch is plentiful. Idioblastic and sheathing sclerenchyma is absent. In the Ceylonese species examined, a vascular cambium is initiated very close to the apical meristem and soon produces a continuous cylinder of secondary xylem and phloem (FIGURE 27). *Acrotrema costatum*, however, exhibits an interrupted stele with wide parenchymatous interfascicular areas (FIGURE 21). In this case, the stem possesses fifteen to twenty collateral bundles each with its own vascular cambium. In the same species, a periderm arises in the inner cortex (FIGURE 21). Current observations on the secondary xylem agree with those already published (Dickison, 1967a). On the transverse section it is often difficult to distinguish vessel elements from fiber-tracheids owing to similar mean diameters and the radial alignment of xylem elements (FIGURE 27). Average vessel element length is 700 μ while the mean length of imperforate tracheary elements is 820 μ. Vessel elements possess scalariform perforation plates with an average of 24 fully-bordered bars. The secondary phloem is composed of sieve tube elements, companion cells and crystal-containing parenchyma. Sieve tube elements correspond to Type III of Zahur (1959) in possessing simple, transverse sieve plates (FIGURE 28). Sieve tube slime is abundant. The nodal anatomy of all Ceylonese species examined is trilacunar (3:3) whereas *A. costatum* is distinguished by a multilacunar condition (ca. 9 traces and gaps).

Root. The epidermal cells are thin-walled and distinguished from the cortex by dark-staining contents. The wide cortex is composed of uniform parenchyma containing starch and raphides. The stele (FIGURE 30) is sharply delimited by an endodermis and 1-layered pericycle. Primary xylem contains a variable number of protoxylem points ranging from triarch to pentarch. Patches of primary phloem are located between the protoxylem poles.

FLORAL ANATOMY

The vascular anatomy of flowers of *Acrotrema* (FIGURES 25, 26) is identical with that described by Wilson (1965) for species of *Hibbertia*. The pedicel of *A. costatum* contains four or five distinct bundles whereas a siphonostele is typical in other species. The sepals are vascularized by three traces which either depart from separate gaps, or result from the trifurcation of a single large bundle which diverges from a single gap. Lateral traces to adjacent sepals are commonly fused along part of their length. The petals are each supplied by a single bundle; which, however,

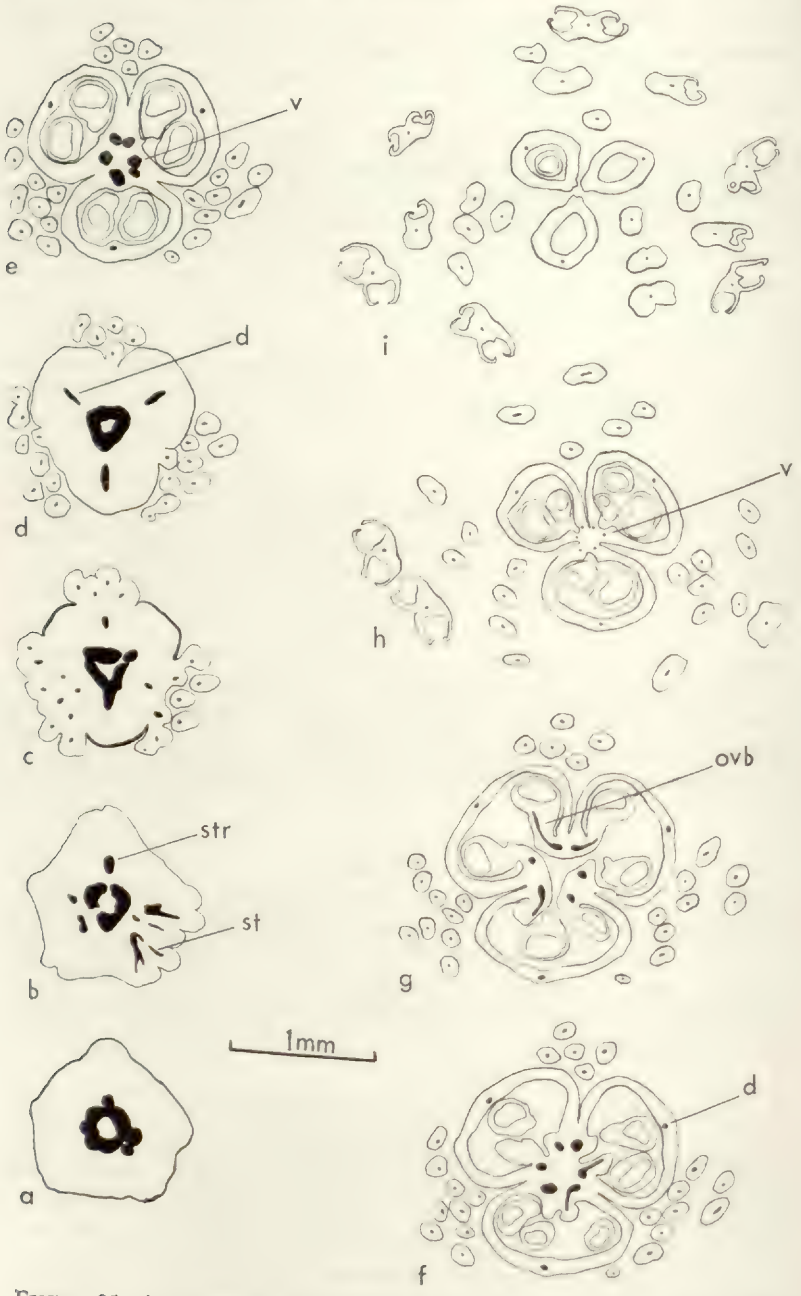


FIGURE 25, *Acrotrema* sp. (*Hoogland 11469*, Ceylon), flower. Drawings of transverse sections through the mature flower from pedicel (a) to stylar region (i) showing details of vasculation. The perianth parts have not been included.

branches soon after entering the petal base. Owing to the flattened receptacle and frequent fusion among perianth traces, it is frequently difficult to follow the course of floral traces as they progress distally in the flower.

Carpels are uniformly vascularized by three bundles, one dorsal and two ventrals. In the Ceylon taxa the receptacle and stele assume a decidedly triangular appearance in transverse section after the departure of perianth and androecial vascular bundles. The dorsal carpel bundles arise from each of the three angles, and terminate at the style apex. The remaining stelar vascular tissue organizes itself into the ventral carpel bundles with the number dependent upon the number of carpels, two or three, in the gynoecium. The ovular supply is derived from the ventral bundles or the ventral bundles terminate within the ovules directly as in *A. costatum*. No evidence of vestigial stelar vascular tissue was observed.

The greatest variation in floral anatomy is found in the vasculation of the androecium, which diverges from the stele in the form of varying numbers of stamen trunk bundles which subsequently divide to produce individual stamen traces (*see* Wilson, 1965). In *A. costatum*, where fifteen stamens encircle the carpels, six to eight concentric stamen trunk bundles arise from the stele. A few of these bundles remain unbranched and directly vascularize individual stamens; more commonly, however, they divide into three or four stamen traces.

In the Ceylonese species studied, the stamens are externally clustered into three fascicles which alternate with the carpels. The androecial vascular supply originates as three strong stamen trunk bundles from the angles of a somewhat triangular stele. Occasionally trunks are double but arise from a single gap. The degree of branching of the main stalk varies from a single bifurcation to five or more divisions depending upon the number of stamens in a fascicle.

POLLEN

The pollen of *A. costatum* (FIGURE 32) has an average size of 22 μ (polar) $\times$ 19 μ (equatorial). Pollen shape is oblate spheroidal and semiangular in polar view. Grains are tectate with the exine thicker at the furrows. Sculpturing is reticulate. Aperture type is tricolpate with furrows that are distinctly granular and narrow.

DISCUSSION

The genus *Acrotrema* exhibits a range of variation in vegetative and floral anatomy of potential phylogenetic and taxonomic significance. Its origin from a woody ancestor seems certain as a result of reduction in cambial activity. However, the limited secondary xylem produced is un-

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d, dorsal carpel bundle; ovb, ovulary bundle; st, stamen trace; str, stamen trunk; v, ventral carpel bundle.

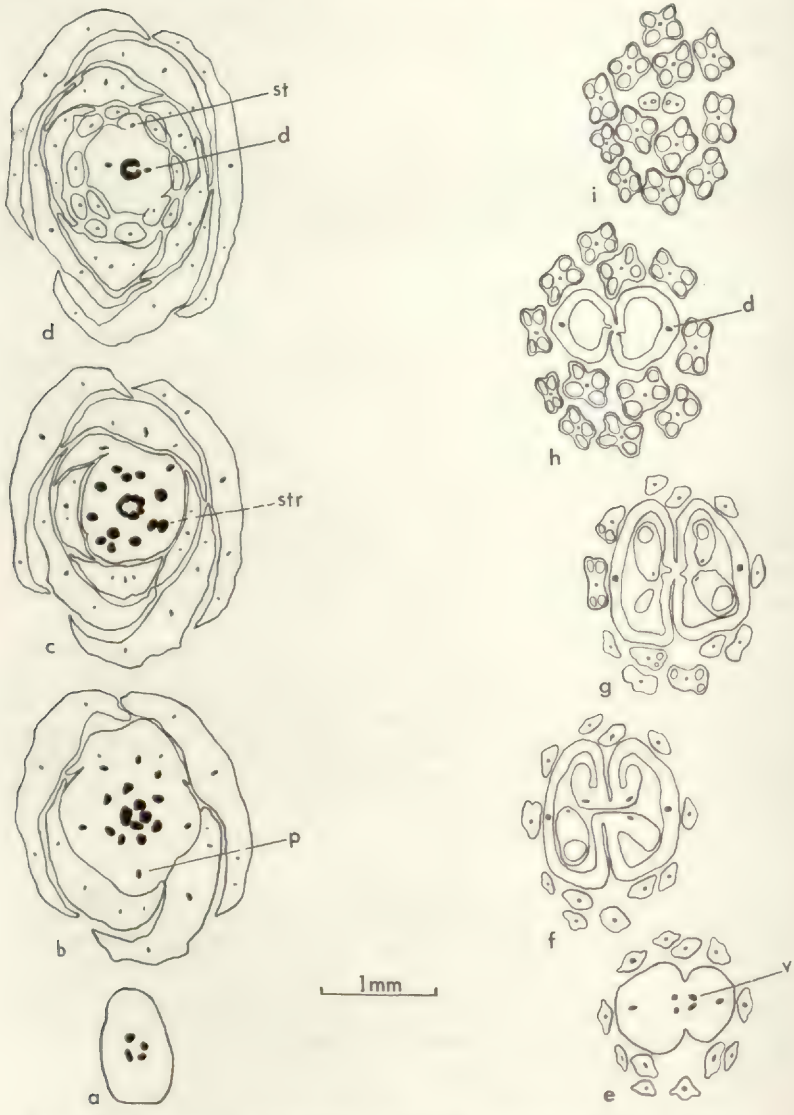

FIGURE 26, *Acrotrema costatum* (*Hoogland 11635*), flower. Drawings of transverse sections through the mature flower from pedicel (a) to stylar region (i) showing details of vasculation. The perianth has not been included in sections e–i. d, dorsal carpel bundle; p, petal trace; st, stamen trace; str, stamen trunk; v, ventral carpel bundle.

usually primitive for a plant of this stature and resembles other members of the subfamily Dillenioideae. The vessel elements have scalariform perforation plates which may be composed of up to nearly fifty

fully bordered bars. Vessel element side wall pitting is scalariform. Imperforate tracheary elements are fiber-tracheids with conspicuous bordered pits. The decrease in length of xylem elements is presumably correlated with a concomitant decrease in length of the cambial fusiform initials.

In addition to the obvious differences in growth habit, and in some cases leaf shape, the genus is distinguished from other Dilleniaceae thus far examined by possessing anisocytic stomata. The Dilleniaceae is now known to contain anomocytic, paracytic, and anisocytic stomata, as well as a specialized pattern called "gordoniaceous." For the most part these patterns are restricted to particular genera. Unfortunately, sufficient information has not been obtained to determine the nature of the primitive stomata. Hallier (1912) was of the opinion that the anomocytic pattern was primitive whereas Takhtajan (1969) has recently suggested that the types with distinctive subsidiary cells are more likely to be unspecialized. Within the Dilleniaceae the anomocytic condition predominates. The occurrence of glandular trichomes of diverse morphology in *Acrotrema* is also especially noteworthy. The only other dilleniaceous genus to have glandular hairs is *Dillenia* (Dickison, 1970a).

The structure of the stem shows no outstanding differences from other Dilleniaceae. The phloem is of a comparatively advanced type with crystal-containing parenchyma present. The range of intrageneric variation, however, is of importance. *Acrotrema costatum* is characterized by a eustele of dissected collateral bundles, multilacunar nodes, and petioles vascularized by a ring of widely spaced bundles. The Ceylon plants examined had a complete vascular cylinder in the stem, trilacunar nodes, and a more complex petiolar anatomy. The course of evolution within the genus remains unclear at this time. No one species or group of species, contains totally unspecialized features.

Wilson (1965) has pointed out that the nature of the stamen trunk androecial vascular supply in the large dilleniaceous genus *Hibbertia* is of possible taxonomic and phylogenetic significance. In his opinion, the following major trends of stamen trunk specialization may be recognized: (1) reduction from numerous stamen trunks (more than 5) to fewer, (2) reduction and eventual disappearance of the main stalk of the stamen trunk, and (3) profusely branching stamen trunks which are more primitive than those with reduced branching. With the above considerations in mind, the following observations may be noted regarding *Acrotrema*. The androecial vasculation of *A. costatum* is significantly distinct from the Ceylonese species studied, as a result of the high number (6–8) of stamen trunks which depart the stele. The degree of branching of the trunks, however, is reduced to usually three and a few of the stalks do not branch at all. None of the stamen trunks have lost their main stalks. The gynoecium shows reduction in carpel number, ovular number, and venation. In contrast, the Ceylonese taxa possess a higher number of stamens which are distinctly fasciculate and are vascularized by three large stamen trunk bundles that branch profusely.

Thus, the evidence from both vegetative and floral organs indicates that while *Acrotrema* is often very divergent in growth habit and gross morphology, the level of anatomical specialization has surprisingly remained comparable to other members of the family. The genus appears only remotely related to extant genera of the Dilleniaceae although anatomically it is most similar to *Dillenia* and *Hibbertia*.

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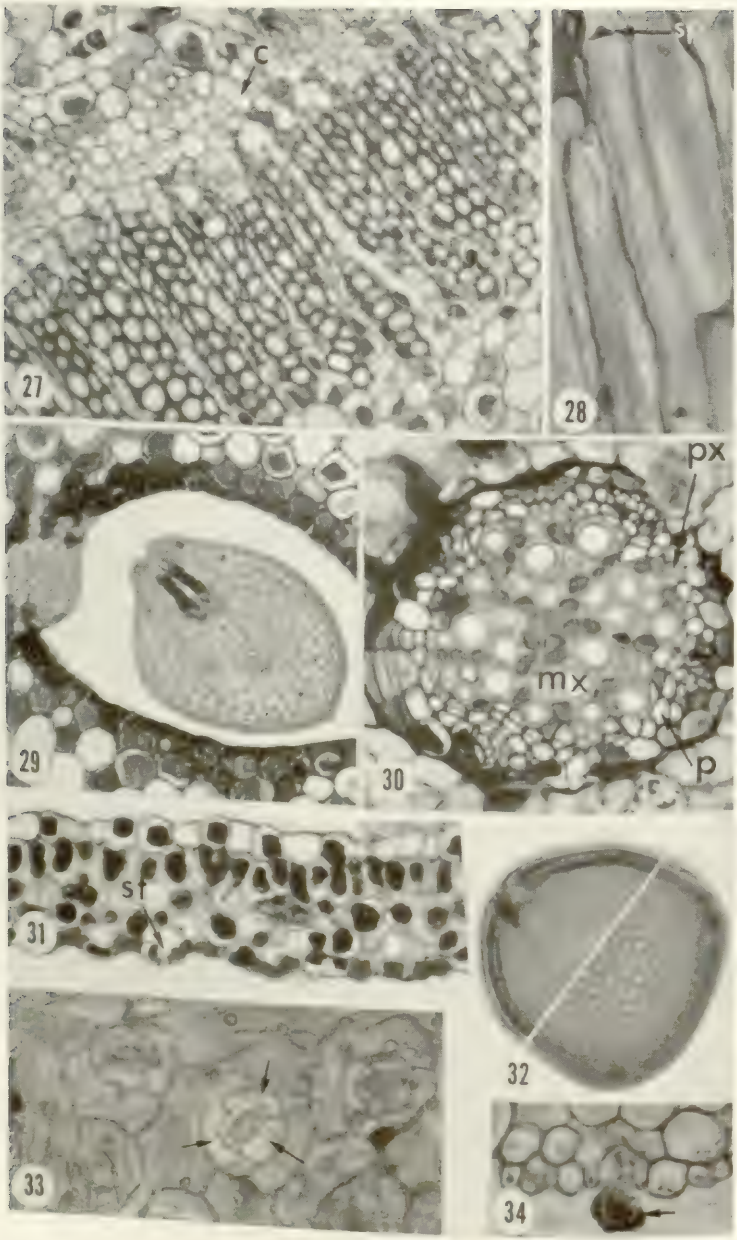
EXPLANATION OF PLATES

PLATE I

FIGURES 27–34. Morphology of *Acrotrema*. 27. Transverse section through the rhizome of *Hoogland 11423* showing cambial zone (c), secondary xylem and phloem, × 156; 28, same, longitudinal section of phloem showing sieve tube element (s) with transverse sieve plates (sp) and abundant slime, × 781; 29, transverse section through the stem apex of *Hoogland 11575* showing conduplicate vernation of youngest leaf, × 156; 30, transverse section through the stele of a root from *Hoogland 11460* showing endodermis (e), pericycle (p), protoxylem (px) and metaxylem (mx), × 312; 31, transverse section of the leaf of *Hoogland 11580* depicting abaxial stomata (st) and weak differentiation into palisade and spongy mesophyll, × 156; 32, pollen of *A. costatum* (*Hoogland 11635*), × 1562; 33, abaxial leaf epidermis of *A. costatum* (from Penang, Malaya *s.n.*) showing anisocytic stomata (arrows point to subsidiary cells), × 156; 34, glandular trichome from the leaf of *A. costatum* (from Penang, Malaya *s.n.*), × 312.

PLATE II

FIGURES 35–43. Herbarium specimens of *Acrotrema* illustrating variation in gross morphology. 35, *A. costatum* (*Smitinand 2999*, US 2211867); 36, *A. uniflorum* var. *rotundatum* (*Thwaites* C.P. *3486*, US 597071); 37, *A. appendiculatum* (*Thwaites* C.P. *3880*, US 1576878); 38, *A. walkeri* (*Thwaites* C.P. *694*, US 1576876); 39, *A. gardneri* (*Thwaites* C.P. *253*, US 597060); 40, *A. lanceolatum* (*Thwaites* C.P. *2660*, US 1576879; 41, *A. thwaitesii* (*Thwaites* C.P. *3969*, US 597067); 42, *A. thwaitesii* (*Thwaites* C.P. *3364*, US 1576882); 43, *A. dissectum* (*Thwaites* C.P. *3393*, US 1576883).



Dickison, Dilleniaceae VII

DICKISON, DILLENIACEAE VII

A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR *

S. M. A. KAZMI

24. **Lindelofia** Lehm. Hamburg. Gart.-Blumenzeit. 6: 351. 1850.

TYPE SPECIES: *L. longiflora* (Benth.) Baill.

Perennial pubescent herb. Basal leaves usually petiolate, cauline leaves alternate, ovate to linear-lanceolate. Inflorescence ebracteate. Calyx usually divided to the base, slightly enlarged and spreading in fruit. Corolla blue, purple or dark purple, cylindrical or cylindrical-campanulate to infundibuliform, lobes usually spreading; faucal appendages usually large, rarely small, trapeziform to oblong, developed at the level of the filaments, or above, on the corolla throat. Stamens 5, anthers large, linear to oblong, usually three times as long as broad, often sagittate; filaments short. Ovary 4-lobed; style long, slender, stigma small. Nutlets depressed-ovoid to depressed-globose, dorsally deeply concave to plane, appendiculate at the margins, appendages subulate and glochidiate at apex, dilated and confluent at base, ventrally attached to a short gynobase.

Species about 12, distributed in northern Iran, Afghanistan, West Pakistan, Kashmir, northwest India, and adjoining areas of URSS and China.

KEY TO THE SPECIES

a. Corolla tube much shorter than the limb, limb divided for 1/3 to 1/2 its length; filaments shorter than the anthers, inserted a little to much below the bases of the faucal appendages. . . . . 1. *L. anchusoides.*

a. Corolla tube equalling to much longer than the limb, limb divided nearly to the base; filaments ± equalling the anthers, inserted adjacent to the bases of faucal appendages.

b. Corolla lobes oblong, faucal appendages very short, much shorter than the anthers. . . . . 2. *L. stylosa.*

b. Corolla lobes ovate, faucal appendages large, equalling or longer than the anthers. . . . . 3. *L. longiflora.*

1. **L. anchusoides** (Lindl.) Lehm. Hamburg. Gart.-Blumenzeit. 6: 352. 1850; Linnaea 24: 216. 1851; Riedl in Rechinger, Fl. Iranica 48: 138. 1967.

Cynoglossum anchusoides Lindl. Bot. Reg. 28: *t. 14.* 1842; A. DC. in DC. Prodr. 10: 151. 1846.

C. emodi Schouw. Ind. Sem. Hafn. Coll. 4. 1846.

* Continued from volume 52, page 136.

C. macrostylum Bunge. Lehm. Reliq. Bot. 412. 1847; Mém. Acad. St. Pétersb. Sav. Étr. **7**: 412. 1851; Boiss. Fl. Orient. **4**: 266. 1875.

Paracaryum heliocarpum Kerner. Ber. Naturw.-Med. Innsbruck 1: [suppl.] 105. 1870; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 161. 1883; Boiss. Fl. Orient. suppl. 354. 1883; Hook. in Curtis's Bot. Mag. **113**: *t. 7520*. 1897.

Adelocaryum anchusoides (Lindl.) Brand. Repert. Sp. Nov. **13**: 548. 1915; Pflanzenr. IV. **252**(Heft 78): 77. 1921.

Lindelofia cynoglossoides Brand. Pflanzenr. IV. **252**(Heft 78): 88. 1921.

Lindelofia aspera Rech. f. Ann. Naturh. Mus. Wien **58**: 48. 1951.

L. macrostyla (Bunge) M. Pop. Fl. URSS. **19**: 627. 1953.

Type: Cultivated from the seeds obtained from Kashmir and Tibet. Herb. East India Company without citation of collector's name, *s.n.* (K).

Icon.: Lindl. l. c. *t. 14*. 1842, under *Cynoglossum anchusoides*; M. Pop. l. c. *t. 35. fig. 1*. 1953, under *Lindelofia macrostyla*; Hook. in Curtis's Bot. Mag. **123**: *t. 7520*. 1897, under *Paracaryum heliocarpum*.

Perennial, erect or rarely decumbent herb, to 100 cm. tall. Stems fistulose, striate, solitary or few with ligneous bases, simple or branched above, covered sparsely or densely with long, soft, usually retrorsely subappressed to appressed trichomes, nontuberculate at base, or sometimes with spreading trichomes arising from tuberculate bases. Basal leaves petiolate, petioles to 18 cm. long, lamina lanceolate, entire, acute, gradually narrowed towards the base, to 25 cm. long, 7 cm. broad, upper surface covered sparsely with soft, long, ± retrorsely subappressed trichomes, lower surface sparsely to densely pubescent in the young leaves, rarely the old leaves covered with stiff trichomes arising from tuberculate bases; cauline leaves short petiolate, lanceolate, to 13 cm. long, 2 cm. broad; upper cauline leaves sessile, lanceolate to linear-lanceolate, to 8 cm. long, 1 cm. broad. Inflorescence terminal and axillary, long pedunculate, geminate or ternate, few flowered. Pedicel erect, to 4(–5) mm. long, in flower, horizontally recurved or slightly reflexed, densely pubescent and 10(–20) mm. long in fruit. Calyx divided nearly to the base, lobes oblong to oblong-ovate, obtuse, densely and uniformly pubescent, 2.5–5 mm. long, to 1 mm. broad in flower, enlarged to 6(–7) mm. long, 1.5(–2) mm. broad in fruit. Corolla pink, blue or purple, campanulate, to 10 mm. long, tube equalling or longer than the calyx, limbs about 1.5 times longer than the tube, divided 1/3 to 1/2 its length, lobes suborbicular; faucal appendages usually puberulous with a prominent medial line, to 2 mm. long, 1 mm. broad at the base, slightly tapering towards the trilobed apex, margins usually ciliate. Anthers to 2 mm. long, 0.5 mm. broad, sagittate; filaments fleshy, shorter than the anthers, inserted at the middle or below the bases of the faucal appendages on the corolla tube. Style ± 9 mm. long, filiform; stigma capitate. Nutlets orbicular to ovate, 4–5(–6) mm. long, 3–4 mm. broad, dorsal surface, usually appendiculate along the medial line and the margins, dorsal appendages generally shorter than the marginal ones, marginal appendages puberulous, triangular, to 2 mm. long, confluent at base and forming a broad marginal wing, usual-

ly more or less inflexed on the dorsal surface; appendages on the lateral and latero-ventral surfaces slightly shorter than the marginal ones.

DISTRIBUTION: Afghanistan, West Pakistan, Kashmir, northwest India, Pamir Alaj, Tien Shan.

West Pakistan: CHITRAL STATE: Brumboret, 2000 m., on Hindukush south, *Bowes Lyon 644* (BM); Ziarat, Lowarai Pass, 2100 m., *Stainton 2552* (BM, E). GILGIT AGENCY: Rama Valley, s.-w. of Astor, 3000 m., *Lankester & Pearson 1453* (BM); Naltar lake, 3500–4000 m., 21 July, 1954, *R. R. Stewart s.n.* (MICH); Gurez Valley, Badwan, 2500 m., *R. R. Stewart 19617* (GH); Chillam Chowki, 3100 m., *Siddiqui, Nasir & Zaffar 4229* (BM); Chhacher pass, 3500 m., *Webster & Nasir 6392* (GH); Astor valley, 2300–2700 m., 23 July, 1892, *Duthie s.n.* (BM); Gilgit, *Toppin 1005* (K); Gubbar, south of Hindukush, 3000 m., *Giles 745* (K); South of Hindukush, *Giles s.n.* (E); South of Astor, 2500 m., *Giles s.n.* (K); Kunslwan (south of Gurez), 2500 m., 21 July, 1876, *C. B. Clarke 29366a, 39388* (K), *29366b* (BM); Kero Lugma Glacier, left bank, 3500 m., *Russell 1319* (BM, GH). HAZARA DIST.: Kaghan Valley: Burawai-Basal road, *Siddiqui 24161* (BM); Naran, 2700 m., *Kazmi 573b* (PES), *Jafri & Ali 3416* (E); between Naran and Saiful Maluk, ca. 2800 m., *Kazmi 802b* (PES). KURRAM AGENCY: Kurram Valley, Hariab, *Aitchison 576* (GH); between Kurram and Kaiwas, *Aitchison 579* (BM). SWAT STATE: Batani, above Ushu, 3000 m., *R. R. Stewart & Rehman 25321* (BM); Kalam, 2200 m., *Rechinger 19424* (W); Utror, 2500 m., *Rechinger 19554* (W); Kulali, 1800 m., *R. R. Stewart 24518* (RAW); without locality, July 1961, *N. A. Malik s.n.* (PES). Reported from: Chitral, Ziarat, *Harriss 16378, 16380* (DD); Gujar, 2550 m., *Harriss s.n.* (DD); Chitral, *Younghusband s.n.*; Barum Gol, Zapotili, 3600 m., *Wendelbo s.n.* (BG).

Kashmir: KISHANGANGA VALLEY: Prope Goroi, 2500 m., *Drummond 15007* (K); near Chorwan, 2700 m., *R. R. Stewart 22625* (GH); Keran, 1200 m., in pond, *R. R. Stewart 17638* (GH); Kishtwar: Machel, sapphire mines, 2600 m., *Ludlow & Sherriff 9126* (BM, GH). LADAKH: Zoji La, 3000 m., *Ludlow & Sherriff 814* (BM); Zoji La Pass, 3300 m., *R. R. Stewart 21249* (GH); Shemsha Karbu, 2850 m., *Ludlow & Sherriff 816* (BM); Dras, 3200 m., *Ludlow & Sherriff 8315* (BM); Dras, 3150 m., *Ludlow & Sherriff 8337* (GH); Dras to Dandal, Sept. 1880, *Young s.n.* (BM); Matayan to Dras, 3000 m., *R. R. Stewart 7444* (K), near Kharbu, 2900 m., *R. R. Stewart 21100* (GH); SIND VALLEY: Sonamarg, 2600 m., *R. R. Stewart 9715* (GH); vicinity of Sonamarg, along Sind River, 50 road-miles east-northeast of Srinagar, 2600 m., *Dickason 90* (MICH); ZANSKAR: Seni, Phe, 3500 m., *Koelz 5808* (GH, MICH); Seni, Hamling, 3500 m., *Koelz 5807* (GH, MICH); Char, Ichor, 4000 m., *Koelz 5681* (GH, MICH); Kangi La to Rangdum, 3500 m., *Koelz 2874* (GH); Oma valley, 3700 m., *Osmaston 193* (K); Mitzahoi, 3300 m., *Rich 1145* (K). Miscellaneous: Himal. bor. occ., regio temp., 8–10000 ped., Herb. Ind. Or. Hook. f. & Thomson, *Thomson s.n.* (BM, GH). Reported from: Sind Valley, *Duthie 11526*.

The trichomes covering the stems and leaves, and the size of calyx and corolla are very variable in *Lindelofia anchusoides*. The trichomes in most cases are long, soft, and appressed in variable densities and give the plant a pale green to greenish appearance. In a few specimens (*Stewart 17638, 21100*; *Young* from Dras to Dandal) the leaves bear shorter, stiff trichomes, arising from large tuberculate bases. This character some-

times is correlated with smaller flowers and shorter pedicels and sometimes not. On examination of more material the plants with stiff, tuberculate trichomes and short pedicels may prove to be a variation worth recognition.

From the other two species of our area, *Lindelofia longiflora* and *L. stylosa*, *L. anchusoides* differs in having a much longer corolla limb compared to the length of the tube, and filaments shorter than the anthers, which are obviously inserted below the bases of faucal appendages.

2. **L. stylosa** (Kar. & Kir.) Brand, Pflanzenr. IV. **252**(Heft 78): 85. 1921; M. Pop. in Fl. URSS **19**: 633. 1953; Riedl in Rechinger, Fl. Iranica **48**: 141. 1967.

Cynoglossum stylosum Kar. & Kir. Bull. Soc. Nat. Moscou **15**: 409. 1842.
Solenanthus nigricans Schrenk ex Fisch. & C. A. Mey. Enum. Pl. Nov. **2**: 29. 1842; DC. Prodr. **10**: 165. 1846; Ledeb. Fl. Rossica **3**: 171. 1847.
Lindelofia benthamii Hook. f. Fl. Brit. India **4**: 159. 1883.

TYPE: In pratensibus subalpinus Alatau ad fl. Sarchan, *Karelin & Kirilow s.n.* (LE-holotype, US-isotype).

ICON.: M. Pop. l. c. *t. 36. fig. 1.* 1953.

Perennial herb, to 60 cm. tall. Stems single to many, striate, simple or branched above, sparsely covered with usually spreading, or sometimes in young plants, retrorsely subappressed trichomes, hardly tuberculate at their bases; old stems sometimes quite glabrous below. Basal leaves lanceolate, entire, acute, narrowed towards the bases into long petioles, including petioles to 35 cm. long, 6 cm. broad; covered on both surfaces with white, subappressed trichomes, to 0.5 mm. long, arising from tuberculate bases; lower cauline leaves subsessile to short petiolate, to 20 cm. long, 1.5 cm. broad; upper cauline leaves few, sessile, linear. Inflorescence terminal, short in flower, to 15 cm. long and paniculately branched in fruit. Pedicels to 7 mm. long in flower, to 22 mm. long and arched out in fruit. Calyx divided to the base, lobes linear-lanceolate, acute, densely covered with subappressed, white trichomes, 6–8 mm. long, 1 mm. broad, slightly enlarged in fruit. Corolla dark purple, tubular to tubular-campanulate, 11–13 mm. long, tube ca. twice as long as the limb, limb divided to 3/5 its length, lobes narrow-oblong to oblong, obtuse to roundish, suberect, 3–5 mm. long, ca. 1.5 mm. broad; faucal appendages, to 1 mm. long and broad, semilunar. Anthers exserted from the corolla tube, 3–3.5 mm. long, 0.5 mm. broad, apiculate, sagittate; filaments fleshy, 1.5 mm. long, inserted on the corolla tube adjacent to the bases of faucal appendages. Style filiform, 13–15 mm. long; stigma capitate. Nutlets 4, broad ovate, to 7 mm. long, 6 mm. broad, dorsal surface glabrous or tuberculate, short appendiculate at the margins and all around, appendages not exceeding 0.7 mm. in length, apices glochidiate, sometimes marginal appendages confluent at their bases forming a very narrow marginal wing.

DISTRIBUTION: Pamir Alaj, Tien Shan, Dsungaro-Tarbagatai, Tibet, Alatau, Afghanistan, West Pakistan, Kashmir, northwest India.

West Pakistan: CHITRAL STATE: Upper Yarkhun valley, 4000–4500 m., *Schmid 2284* (MICH). GILGIT AGENCY: Baltistan, upper end of Hushe valley, Ghondakoro glacier basin at the foot of Mesherbrum, 3500–4000 m., *Webster & Nasir 6077, 6102* (GH).

Kashmir: LADAKH: Shelshel river, 4300 m., *Strachey & Winterbottom 2* (GH); Hunnupatta, 3500 m., *Osmaston 49* (K); Tsaka La, 4500 m., in dry ravine, *Koelz 2369* (GH); Bod Kharbu, Treaty Road, 3300 m., *Ludlow & Sherriff 8368* (GH); Zanskar: Kangi La to Rangdum, 3500 m., *Koelz 2874* (GH); Sulle to Padum, *Schlagintweit 6708* (GH); top of the Pentse La Pass (pass between Zanskar and Dras), *Schlagintweit 7476* (GH).

Brand [Pflanzenr. IV. 252(Heft 78): 87. 1921] considering *Lindelofia benthamii* Hook. f. (*l. c.*) identical to *L. angustifolia* (Schrenk) Brand, l. c. IV. 252(Heft 78): 87. 1921, cited a number of specimens from our area. In fact *L. benthamii* is a synonym of *L. stylosa* and agrees in all its details with the latter. *L. stylosa*, is distinguished from *L. angustifolia* by having distinct faucal appendages in the corolla throat, whereas such appendages are totally absent in *L. angustifolia*. I did not see any specimen of *L. angustifolia* from West Pakistan, Kashmir or northwest India and its occurrence in these areas appears to be quite doubtful. The specimen (*Schlagintweit 6708*) cited by Brand belongs to *L. stylosa*.

Lindelofia stylosa is closely related to *L. longiflora* from which it is distinguished by having narrower corolla lobes and very short faucal appendages.

3. **L. longiflora** (Benth.) Baill. Hist. Pl. **10**: 379. 1890; Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. **3a**: 103. *t. 42, fig. A–C*. 1893; Brand, Pflanzenr. IV. **252**(Heft 78): 85. 1921.

Cynoglossum longiflorum Benth. in Royle Illustr. Bot. Himal. Mount. 305. 1839; Lindl. Bot. Reg. **26**: *t. 50*. 1840.
Omphalodes longiflora A. DC. in DC. Prodr. **10**: 158. 1846.
Paracaryum longiflorum Boiss. Diagn. Pl. Orient. **11**: 132. 1849.
Lindelofia spectabilis Lehm. in Hamb. Gart.-Blumenzeit. **6**: 352. 1850; Linnaea **24**: 216. 1851; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 159. 1883.

TYPE: Cashmere, *Royle s.n.* (K?).

ICON.: Lindl. Bot. Reg. **26**: *t. 50*. 1840.

Perennial herb, to 60 cm. tall. Stems usually solitary, sometimes few, simple, covered sparsely to densely with white, crisped, spreading to subappressed trichomes, to 1.5 mm. long, some from tuberculate bases others not. Basal leaves lanceolate, entire, acute, attenuate towards the base into petioles, usually shorter, sometimes equal or rarely longer than the lamina, including petioles to 18 cm. long, 8 cm. broad, sparsely to densely covered on both surfaces with subappressed to erect trichomes, more or less like those on the stem; cauline leaves very variable, lower cauline leaves ses-

sile, oblong-lanceolate to ovate, acute, at the bases slightly dilated, more or less rounded or subcordate; upper cauline leaves semiamplexicaul, shorter and narrower than the lower ones. Inflorescence terminal or subterminal, short in flower, later elongated to 15 cm. Pedicel erect, to 5 mm. long in flower, pubescent, elongated up to 12 mm., horizontal to subreflexed in fruit. Calyx divided to the base or connate for its lower 1/4, 7 mm. long in flower, lobes oblong to ovate, obtuse to subacute, ca. 3.5 mm. broad, variously hairy, to 10 mm. long, lobes 5.5 mm. broad in fruit. Corolla bright to deep blue to purple, campanulate-infundibuliform, tube to 13 mm. long, limbs to 6 mm. long, divided nearly to the base, lobes ovate, spreading; faucal appendages to 4 mm. long, 2 mm. broad, sometimes slightly tapering toward the more or less emarginate apex, margins ciliate. Anthers ca. 2 mm. long, 0.5 mm. broad, more or less rounded at both ends; filament ca. 2 mm. long, fleshy, inserted adjacent to the bases of the faucal appendages on the corolla tube. Nutlets ovate, excluding appendages to 4 mm. long, 2.5 mm. broad, margins appendiculate, appendages to 2 mm. long, glochidiate at apex, dilated at base, free or confluent forming a narrow marginal wing, spreading, rarely inflexed on the concave dorsal surface, which has a more or less prominent medial ridge, bearing few to many vertical appendages similar to the marginal ones. Style to 15 mm. long, filiform; stigma capitate.

Distribution of species: West Pakistan, Kashmir, northwest India.

Key to the Varieties

a. Upper cauline leaves broad-lanceolate to ovate; calyx lobes with prominent midrib, bearing long crisped trichomes usually only on the midrib and margins. ..... 3b. var. *levingii*.
a. Upper cauline leaves lanceolate; calyx lobes with inconspicuous midrib, bearing short trichomes usually all over the surface and margins.
  b. Calyx lobes subacute to acute at apex, lobes uniformly pubescent on the dorsal surface. ..... 3c. var. *falconeri*.
  b. Calyx lobes obtuse to roundish at apex, densely pubescent on the margins with short trichomes, and uniformly pubescent on the dorsal surface. ..... 3a. var. *longiflora*.

3a. Var. longiflora.

Leaves on the upper surface sparsely covered with subpatent, long trichomes, arising from tuberculate bases, densely covered on the lower surface with subappressed, crisped, soft trichomes, not tuberculate at their bases, to 0.3 mm. long. Calyx usually divided for 3/4 of its length or sometimes to the base, lobes to 7 mm. long, 3.5 mm. broad in flower, enlarged to 10 mm. long, 5.5 mm. broad in fruit, with inconspicuous midrib, covered densely over the dorsal surface with long, white trichomes, usually longer on the middle and towards the base, margins very densely pubescent with trichomes to 0.2 mm. long, ventral surface more or less pubescent, usually on the upper parts and margins. Corolla dark blue, in-

fundibuliform, tube to 13 mm. long, limb to 7 mm. long; faucal appendages comparatively narrower and shorter than in var. *levingii*.

West Pakistan: CHITRAL STATE: Brumboret, *M. A. Siddiqui & A. Rehman 26853* (BM). GILGIT AGENCY: Kamri Pass, 3000–3500 m., *Duthie 12581* (BM); Baltistan, 2700 m., *Hunter-Weston 10251* (MICH). HAZARA DIST.: Kaghan Valley, Saiful Maluk, *Shaukat Ali 129* (BM).

Kashmir: Tragbal, 19 July 1876, *C. B. Clarke 29226* (K), 3200 m., Sept. 1913, *Evershed s.n.* (BM), *Duthie 13524* (K); Rajdhiangan Pass, *R. R. & I. D. Stewart 18005* (GH), 3000–3500 m., *R. R. Stewart 19517* (GH), 3000 m., *R. R. Stewart 19307* (GH); Sonamarg, 3300 m., *R. R. Stewart 6560* (K), *9801A* (GH); Sind Valley, 3000 m., *Stainton 5026* (BM); vicinity of Sonamarg, on the Sind river, 50 road-miles east-northeast of Srinagar, 4000 m., *Dickason 91* (MICH); Gangangir, Sind Valley, 3200 m., *Ludlow & Sherriff 7971* (BM, GH), *7979* (GH); Gumber valley in Sind Valley, 3300 m., *Ludlow & Sherriff 7636* (GH); Sekiwas, Yamkar Pass, 3500 m., *R. R. Stewart 12552* (GH); Mengandob, 3300 m., *Polunin 56/724* (BM); Butin Pandsab, Wangat Valley, 3300 m., *Pinfold 269* (BM); Dras Valley, Zoji La, 2 June 1870, *Henderson 324* (K); Gangabal Lakes, 3000 m., *R. R. & I. D. Stewart 4552* (MICH); Zaiwan, 3000 m., *Polunin 56/603* (BM); near Karagbal, 2700 m., *R. R. Stewart 22559* (GH); Allyabad, Pir Panjal, *Inayat 25720* (K); Surgun, 3200–4000 m., *Schmid 549* (BM); Budnambal, 4000 m., *Fuller 226* (K); Mantar Valley, near Desu, 3000 m., *Ludlow 95* (BM). Miscellaneous: Kashmir, *Price 72A* (K), *Coventry 577* (K).

The typical variety is very variable in the form of its leaves. Generally the basal leaves have long petioles; the cauline leaves are oblong-lanceolate, acute, usually narrowed at both ends and truncate, roundish or subamplexicaul at base. The lower surfaces are densely covered with short trichomes to sometimes slightly pubescent. All the trichomes lack tuberculate bases. These characters are well correlated with the ovate, obtuse calyx lobes densely ciliate at the margins. The corolla tube is narrower than that of var. *levingii*. Corollas in almost all the collections are deep blue rather than purple.

3b. Var. **levingii** (C. B. Clarke) Brand, Pflanzenr. IV. 252(Heft 78): 85. 1921.

Lindelofia spectabilis var. *levingii* C. B. Clarke in Hook. f. Fl. Brit. India **4**: 159. 1883.

L. platycalyx Riedl in Køie & Rechinger, Biol. Skr. 13(4): 202. 1963, in Rechinger, Fl. Iranica **48**: 140. 1967, *syn. nov.*

TYPE: Kashmir: Pir Pingul, alt. 11500 ft., *Levinge s.n.* (K).

ICON.: Riedl, l. c. *fig. 153.* 1963, under *Lindelofia platycalyx*.

Leaves sparsely covered on both surfaces with trichomes arising from tuberculate bases; calyx shape more or less like that of the typical variety; calyx lobes with prominent midrib, covered sparsely or densely, usually on the midrib and margins, with crisped trichomes, to 0.5 mm. long, internally usually glabrous. Corolla mostly purple to sometimes dark

blue, campanulate-infundibuliform, tube to 10 mm. long, limbs 5–6 mm. long, divided nearly to the base; faucal appendages to 4 mm. long and 2 mm. broad.

West Pakistan: GILGIT AGENCY: Upper Astor Valley, Kalapani to Shankargarh, 3300 m., *R. R. Stewart 22745a* (GH). HAZARA DIST.: Ihadal (Shadal), 16 Aug. 1899, *Inayat s.n.* (W-type of *L. platycalyx* Riedl); Kaghan Valley, between Balakot and Babusar Pass, *Abel 134* (BM); between Shogran and Sari Rest House, 2500 m., *Kazmi 2158* (PES); northeast of Saiful Maluk Sar, 3570 m., *Schmid 331* (BM, E); Saiful Maluk, *Shaukat Ali 129* (BM, mixed with var. *longiflora*).

Kashmir: Pir Panjal, 3300 m., *Levinge, s.n.* (K-type); Pir Panjal Pass, 3200 m., *Ludlow 31* (BM); Banihal Pass, Pir Panjal Range, 2575 m., *R. R. Stewart 12203, 14709* (GH); Gulmarg, 2750 m., *Duthie 13045* (BM), 3000 m., *R. R. Stewart 10395* (GH), 2700 m., *Tamin 158* (BM); Gulmarg, Nagini, 2700 m., *R. R. Stewart 14843a* (GH); Killanmarg, above Gulmarg, 3000 m., *R. R. Stewart 10420A, 8665* (GH); Pahlgam, *R. R. & I. D. Stewart 5904* (MICH); vicinity of Kolahoi mountains and glacier, about 50 miles north of Islamabad, via Pahlgam and Arau, *Dickason 94* (MICH); Tuleon, above Pahlgam, 3200 m., *R. R. Stewart 21844a* (GH); Tuleon Way, east of Pahlgam, on east Lidder river, 27 road-miles north of Islamabad, 2700 m., *Dickason 93* (MICH); Shisha Nag, 3500 m., *Coventry 645* (K); Lidderwat, 3000 m., *Coventry 577* (K); Sinathan Pass, 3500 m., *Ludlow & Sheriff 9291* (BM, GH); Ningle Nullah, *Pinfold 217* (BM). Miscellaneous: Kashmir: *R. R. Stewart 12957* (BM), 2700 m., 1957, *Mrs. Prescott-Decie s.n.* (BM).

The variety *levingii* of *Lindelofia longiflora* is very variable in the size and form of leaves, but generally the cauline leaves are much broader and shorter compared to those of the other two varieties. The leaves are always sparsely pubescent on both surfaces. These characters are correlated with the pubescence of the calyx lobes, which are covered only on the midrib and the margins with long, crisped white trichomes. The corolla in this variety is comparatively broader and more or less campanulate in form, bearing longer faucal appendages compared to the corolla in the other two varieties.

Lindelofia platycalyx agrees in all its details to *L. longiflora*.

3c. Var. **falconeri** (C. B. Clarke) Brand, Pflanzenr. IV. 252(Heft 78): 85. 1921.

Lindelofia spectabilis Lehm. var. *falconeri* C. B. Clarke in Hook. f. Fl. Brit. India **4**: 159. 1883.

TYPE: KASHMIR: *Falconer s.n.* (K-Herb. Late East India Co., holotype, GH-isotype).

Leaves very similar to those of var. *longiflora*; calyx obviously divided to the base, lobes oblong-lanceolate, acute to subacute, to 6 mm. long, 1.5 mm. broad in flower, enlarged to 10 mm. long and 3 mm. broad in fruit; corolla as that of var. *longiflora*.

West Pakistan: GILGIT AGENCY: Burzil Pass, north slope, 3300 m., *R. R.*

Stewart 22004 (GH), south slope, *R. R. Stewart 19126* (GH); Kamri Pass, 4000 m., *Giles 700* (K); Mir Panzil Pass, ascent to the Deosai, 3300 m., *R. R. Stewart 19985* (GH). Miscellaneous: Gilgit-Chitral, *Leichtlin s.n.* (K, received in herb. on July 1889).

Kashmir: Koragbal, north slope, Rajdhiangan Pass, ca. 2750 m., *R. R. Stewart 22586c* (GH); Sonamarg, 3000 m., *R. R. Stewart 9858A* (GH); vicinity of Sonamarg, on Sind river, 50 road-miles east-northeast of Srinagar, 3500 m., *Dickason 92* (MICH); above Gulmarg, 3000 m., *R. R. Stewart 10329* (GH); Koslorkut, 8 miles n.w. of Vishensar, 3300 m., *Polunin 56/701* (BM). Miscellaneous: Kashmir, *Falconer s.n.* (K, GH, types).

Lindelofia longiflora var. *falconeri* can very easily be distinguished from the other two varieties of the species by its lanceolate, acute to subacute calyx lobes. In the type specimen the upper cauline leaves are narrower than in any of the other specimens cited. In the other collections the cauline leaves are usually oblong-lanceolate and broader than those in the type specimen.

25. **Cynoglossum** L. Sp. Pl. 134. 1753; Gen. Pl. ed. 5. 65. 1754.

TYPE SPECIES: *C. officinale* L. (Lectotype).

Usually perennial or biennial, rarely annual herbs. Calyx usually divided to the base, slightly enlarged in fruit. Corolla cylindrical to campanulate-infundibuliform; limbs divided to the middle or to the base, lobes usually ovate; faucal appendages usually subquadrate, rarely oblong to semilunar. Stamens included; anthers usually ovoid to oblong-ovoid, at maximum three times as long as broad, usually shorter; filaments usually inserted at the middle or rarely above the middle of the corolla tube. Style fleshy or filiform of different lengths, stigma capitate. Nutlets 4, forming a much depressed pyramid, ovoid to globose, appendiculate at the margins or all around, appendages glochidiate at apex, free at the base to sometimes dilated and confluent forming narrow or broad marginal wings, attached to the gynobase by ventral scars, usually developed on the upper half of the ventral side.

Species about 60, distributed all over the world, except in arctic regions.

KEY TO THE SPECIES

a. Nutlets 2–3 mm. long.
   b. Styles filiform, long, cylindrical; nutlets roundish to ovate, usually dorsally concave, rarely convex, variously appendiculate, appendages of equal or various lengths, marginal ones usually confluent at their bases and forming narrow to broad wings. . . . . 3. *C. wallichii.*
   b. Styles fleshy, thick, short, ± 4-angled; nutlets roundish, dorsally convex, uniformly appendiculate, appendages ± of equal length, usually not confluent at their bases.
      c. Leaves uniformly covered dorsally with trichomes, to 0.2 mm. long, not arising from tuberculate bases. . . . . 2. *C. zeylanicum.*

c. Leaves covered dorsally with trichomes of unequal lengths, usually longer than 0.2 mm., obviously arising from tuberculate bases. . . . . 1. *C. lanceolatum.*

a. Nutlets 3.5–5 mm. long.

d. Basal leaves petiolate, lamina ovate, abruptly narrowed at the base, truncate or rarely subcordate. . . . . 4. *C. stewartii.*

d. Basal leaves petiolate, lamina oblong, gradually attenuate at the base towards the petioles.

e. Cauline leaves oblong, obtuse to subacute, gradually narrowed towards the bases. . . . . 5. *C. nervosum.*

e. Cauline leaves ovate, acute to acuminate, roundish at base. . . . . 6. *C. microglochin.*

1. **C. lanceolatum** Forssk. Fl. Aegypt.-Arab. 41. 1775; DC. Prodr. **10**: 149. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 156. 1883; Brand, Pflanzenr. IV. 252(Heft 78): 137. 1921, excl. vars.; Riedl in Rechinger, Fl. Iranica **48**: 145. 1967.

C. micranthum Desf. Tab. Ecole Bot. ed. 1. 220. 1804.
C. hirsutum Jacq. Hort. Schönbr. **4**: *tab. 489.* 1804.
C. canescens Willd. Enum. 180. 1809.
C. racemosum Roxb. Hort. Beng. 13. 1814; Fl. Indica, ed. Carey, **2**: 6. 1824.
C. platyphyllum Klotzsch in Peter, Reise Mozambique Bot. 254. 1862.
C. abyssinicum Hochst. & Vatke ex Engler, Abh. Preuss. Acad. Wiss. 1891. **2**: 353. 1892.
C. johnstoni Baker, Kew Bull. **1894**: 29. 1894.

TYPE: Hadie, *Forsskål s.n.* (C).

ICON.: Brand, l. c. *fig. 18, A–G.* 1921.

Erect biennial or perennial herb, 60–150 cm. tall. Stems woody at base, branched, branches long, spreading; densely covered with stout, white trichomes arising from tuberculate bases up to 2 mm. long, trichomes on the upper part of the stem comparatively shorter and ± subappressed. Basal leaves petiolate (petioles to 8 cm. long), lanceolate, entire, acute, attenuate at the base, including the petioles to 30 cm. long and 4 cm. broad, nerves on the upper surface inconspicuous, raised and prominent below, upper surface covered uniformly with thin, subappressed trichomes, intermixed in different densities with longer, thicker trichomes to 1 mm. long, arising from large tuberculate bases, sometimes surrounded with tiny white tubercles, lower surface covered more densely, especially on the nerves, with similar trichomes; cauline leaves subsessile to short petiolate, to 12 cm. long and 2 cm. broad; upper cauline leaves sessile, much reduced in size. Inflorescence axillary or terminal, bifurcate to dichotomously branched, branches spreading, ebracteate, short, scorpioid in flower, elongated to 25 cm. when in fruit. Pedicels to 0.1 mm. long in flower, to 2 mm. long and usually reflexed in fruit. Calyx divided to the base, lobes ovate, obtuse, densely hairy externally, glabrous within, ± 1 mm. long, enlarged and spreading in fruit, to 2 mm. and 1 mm. broad. Corolla light blue, 2–3 mm. long, limbs divided to the

base, lobes ovate; faucal appendages broader than long. Stamens included, anthers ovate, minute, filaments short. Nutlets 4, ovate, 1–2 mm. long, ± equally broad, dorsally convex, appendiculate all around, appendages of equal length, vertical, not confluent at base, apex glochidiate. Style short, fleshy, 0.5–0.7(–1) mm. long in fruit.

DISTRIBUTION: Africa excluding the northwestern parts, Arabia, Pakistan, Kashmir, India, Nepal, Burma, Thailand, Philippines, Formosa, Riu Kiu, and China.

West Pakistan: DIR STATE: Dir village, 1500 m., *Salim 105* (K). HAZARA DIST.: Tribal area, Nilishang, ca. 1200 m., *Burtt 1426* (E); Kaghan valley, between Balakot and Babusar Pass, *Abel 13* (BM); Siran Valley, Jabori, *Burtt & Arshad Ali 778* (E). KURRAM AGENCY: Kurram Valley, *Afandi 671a* (PES). RAWALPINDI DIST.: Khangah to Sangla Hills, *R. R. Stewart 1457* (K); near Rawalpindi, 600 m., *R. R. Stewart 16521a, 13787* (GH); Rawalpindi, 500 m., *R. R. Stewart 12958* (K, GH, RAW). SWAT STATE: Near Bahrain, *R. R. Stewart 25406* (BM); near Madian, ca. 1500 m., *Rodin 5551* (US), *Kazmi s.n.* (PES). Miscellaneous: Bank of Chenab, Oct. 1846, *Thomson s.n.* (K); Western Himalaya, May 1832, *Gerard s.n.* (BM).

Kashmir: Bandipur, 1500 m., *R. R. Stewart 22521* (GH); Ganderbal, *R. R. Stewart 7497* (K); Gund, 2000 m., *Rich 278* (K); Chokoti to Uri, Aug. 1880, *Young s.n.* (BM). Miscellaneous: Himal. bor. occ. 3–7000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH, MICH).

2. **C. zeylanicum** (Vahl) Thunb. ex Lehm. Neue Schriften Naturf. Ges. Halle 3(2): 20. 1817; Asperif. 116. 1818; Brand, Pflanzenr. IV. 252(Heft 78): 134. 1921, excl. var. *lanceolatum* C. B. Clarke; Riedl in Rechinger, Fl. Iranica **48**: 145. 1967.

Anchusa zeylanica Vahl ex Hornem. Enum. Hafn. 3. 1807, Hort. Hafn. 1: 176. 1813, *nomen nudum*.

Echinospermum zeylanicum Lehm. Asperif. 116. 1818; A. DC. in DC. Prodr. **10**: 142. 1846.

Rochelia zeylanica Roem. & Schult. Syst. **4**: 108, 780. 1819.

Cynoglossum furcatum Wall. Cat. No. 919. 1828, *nomen nudum*; ex Roxb. Fl. Indica, ed. Carey, 2: 6. 1824; DC. Prodr. **10**: 149. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 155. 1883.

Cynoglossum coeruleum Buch.-Ham. ex D. Don, Prodr. Fl. Nepal. 100. 1825.

C. micranthum Desf. var. *decurrens* Trimen, Handb. Fl. Ceylon 3: 203. 1895.

TYPE: not indicated.

ICON.: Wight, Icon. Pl. Indiae Orient. **4**: *t. 1395*. 1850, under *C. furcatum*.

Biennial erect herb, to 85 cm. tall. Stems brownish, fleshy, simple or branched, covered densely with thick yellow to brownish, antrorsely appressed to subappressed trichomes. Basal leaves petiolate, lamina oblong to elliptic, obtuse to subacute, 15–20 (–30) cm. long, 35–85 mm. broad, narrowed towards the base into petioles to 12 cm. long, nerves prominent below, covered uniformly on both surfaces with nonpungent

trichomes to 0.2 mm. long, not arising from conspicuous tuberculate bases; cauline leaves short petiolate, upper cauline leaves sessile, oblong-lanceolate, gradually reduced in size upwards. Inflorescence terminal or subterminal, short in flower, ebracteate and elongated in fruit. Pedicel shorter than the calyx in fruit. Calyx divided for 3/4 of its length, lobes ovate, 3–4 mm. long, obtuse to roundish at apex, covered with trichomes like those on the leaves. Corolla blue, infundibuliform, 5 mm. long, limbs 8–9 mm. in diameter, divided nearly to the base; faucal appendages blue, subquadrate, larger than the anthers. Style fleshy, much shorter than the calyx. Nutlets 4, ovoid, 3–4 mm. long, uniformly appendiculate all around, emarginate, appendages glochidiate at apex, free at base, dorsal surface convex.

DISTRIBUTION: Afghanistan, Pakistan, India, Ceylon, Philippines, Japan, China.

West Pakistan: Reported from Swat: inter Madyan et Kalam, 1700 m., *Rechinger 19377* (W).

I did not see a specimen of this species from Afghanistan or West Pakistan; its distribution in these areas needs thorough investigation.

3. **C. wallichii** G. Don, Gen. Syst. **4:** 354. 1838; A. DC. in DC. Prodr. **10:** 150. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4:** 157. 1883.

C. stellatum Wall. Cat. No. 924. 1828, *nomen nudum.*
C. canescens Wall. Cat. No. 918. 1828, *nomen nudum.*
C. calycinum Wall. Cat. No. 923. 1828, *nomen nudum*, non C. A. Meyer.
C. vesiculosum Wall. Cat. No. 920. 1828, *nomen nudum.*
C. edgeworthii A. DC. in DC. Prodr. **10:** 150. 1846.
C. denticulatum A. DC. in DC. Prodr. **10:** 150. 1846.
C. micranthum Hook. f. & Thoms. ex C. B. Clarke in Hook. f. Fl. Brit. India **4:** 157. 1885.

TYPE: Native of Nepaul, in Gosainsthan, *Wallich 923* (K).

Erect biennial herb, to 75(–100) cm. tall. Stems solitary to many, striate, usually branched above, branches long, divaricate; stem and branches in the lower parts covered densely with spreading, white trichomes to 3 mm. long, arising from tuberculate bases, in the upper part with shorter, sometimes subappressed ones. Basal leaves petiolate, including petioles, to 17 cm. long and 32 mm. broad, lamina usually shorter, sometimes equalling or longer than the petiole, lanceolate to obovate, obtuse to acutish, gradually narrowed at base, nerves on the upper surface sunken, on the lower surface raised and prominent, both surfaces densely covered with long, spreading, white trichomes, usually arising from large, prominent tuberculate bases, trichomes on the margins of petioles are sometimes even longer; lower cauline leaves acute, usually longer and broader than the basal ones and with much shorter petioles; middle and upper cauline leaves subsessile to sessile, gradually reduced

in size upwards. Inflorescence terminal or axillary, usually geminate, branches divaricate, ebracteate, short scorpioid, bearing closely set flowers, much elongated after flowering, with fruits to 20 mm. apart. Pedicels none to very short in flower, hairy, reflexed to 3 mm. long in fruit. Calyx divided to the base, lobes oblong, erect, ca. 2 mm. long and 0.5 mm. broad, slightly enlarged in fruit, spreading, densely pubescent to sometimes ciliate at the margins, rarely with the trichomes arising from minute tubercles. Corolla pale to deep blue, campanulate, 3.5–4 mm. long, tube ± equalling the calyx, limbs equalling the tube, divided nearly to the base, lobes rounded; faucal appendages subquadrate, slightly emarginate, puberulent. Anthers ovate, 0.8 mm. long, 0.4 mm. broad; filament short, inserted nearly at the middle of the corolla tube. Nutlets ovate, apex roundish to acute, excluding the appendages, 2–2.5 mm. long, 1.5–2 mm. broad, dorsally concave, bearing few to many vertical glochidiate appendages, margins appendiculate with the appendages more or less confluent at their bases and usually forming a marginal wing, appendages on the ventral side like those on the margins, not confluent at bases and usually smaller.

DISTRIBUTION: Afghanistan, Pakistan, Kashmir, Pamir Alaj, India.

3a. Var. **wallichii**.

Dorsal surface of the nutlets broad-ovate, sunken, sparsely to densely covered with vertical appendages, dorsal longitudinal keel not conspicuous, apex roundish, marginal appendages many, long, dilated and confluent at base forming broad elevated wings.

West Pakistan: CHITRAL STATE: Brir, 1200 m., *Siddiqui & Rahman 26851* (BM). GILGIT AGENCY: Naltar Valley, 2000 m., *Duthie 12437* (BM); BALTISTAN: Skardu to Shigar, 2000 m., *R. R. Stewart 20480* (GH); Skardu, 1900 m., *R. R. Stewart 20469* (GH); right side of the Shayok via Kiris to Neru on the right side of Indus, *Schlagintweit 5827* (GH); south of Satpara Lake, ca. 4.5 miles south of Skardu, 2000 m., *Webster & Nasir 5841* (GH); Skardu, 1800 m., *Webster & Nasir 5449* (GH); upper end of Hushe Valley, Ghondakoro Glacier basin at the foot of the Masherbrum, 2500 m., *Webster & Nasir 6045* (GH); Rattu, Kamri Nala, Astor, 8 July 1901, *Duthie s.n.* (K); Rupal to Gorikot, 1700 m., *R. R. & I. D. Stewart 18911* (GH); Shinger, 1900 m., *R. R. Stewart 20543* (GH); Pranu, 2500 m., *Koelz 9701* (GH); Skardu, 2500 m., *Schlagintweit 840* (US); Ashkoley, 3000 m., *Clarke 30408* (K); Gilgit, *Toppin 1038* (K); KARAKORAM: Kero Lugma Glacier, 3000–3500 m., *Russell 1337* (BM); Kushuchun Lugma Valley, 3000–3500 m., *Russell 1776* (BM). HAZARA DIST.: Kaghan Valley, Saiful Maluk, ca. 3000 m., *Kazmi 799A* (PES), *Shaukat Ali 133* (BM); Balakot, 1000 m., *Jafri & Ali 3267* (E); Shogran to Sari Rest House, ca. 2500 m., *Kazmi 686B* (PES); Sarul, *Inayat 22034* (K); Shinu, *Inayat 22035* (K); Tribal territory, Ganja Kandoo to Hill Durra Nullah, 3000 m., *Burtt & Kazmi 1259* (E). KURRAM AGENCY: Kurram Valley, Parachinar, *Barbour s.n.* (BM), *Afandi 671* (PES). RAWALPINDI DIST.: Rawalpindi, 1960, *McVean s.n.* (E); MURREE HILLS: near Rosenheim, 2000 m., *Rodin 5360* (US). QUETTA DIST.: Ziarat, *Lace 3401* (E). SWAT STATE: Sho Nala, *Rahman 26* (BM).

Kashmir: Gulmarg, 2700 m., Sept. 1922, *Barbour s.n.* (BM), 3500 m., Aug. 1922, *Barbour s.n.* (BM); Purig, Tangola, *Koelz 6075* (US); Parkachen, *Koelz 5977* (MICH, GH, US); Pahlgam, Lidder Valley, 2000 m., *R. R. Stewart 21623* (GH); Pahlgam, 2100 m., *R. R. Stewart 21628, 21762* (GH); Islamabad, 17 Nov. 1896, *H. H. Johnston 2* (E); Kootihar Valley, 3 Dec. 1896, *H. H. Johnston s.n.* (E); Banks of Jhelum below Islamabad, ca. 2000 m., *Duthie 13059* (K); Kajei-utholi, Padar, upper Chenab, 2000 m., *R. R. Stewart 2925* (K), *2919* (K, US); Upper Chenab Valley, *Ellis* in *Gamble 189* (K); Goochi, 2000 m., *Fuller 172* (K); Kuihama Range, Nagmarg, 3000 m., *Fuller 72b* (K); Rambar, Jammu-Kashmir Road, ca. 1000 m., *R. R. Stewart 12964* (GH); Gurez across the Ulli plain and two small passes to Bandipur, northwest of Srinagar, *Schlagintweit 12082* (GH); Baramula, along both sides of Jhelum Valley down to Mera, 1800–2000 m., *Schlagintweit 12469* (GH); environ of Srinagar, within a circle of 8 miles, *Schlagintweit 4503* (US), *4237* (GH); Sonamarg, 2500–3000 m., *R. R. Stewart 6280* (K); Sonamarg to Kulan, Sept. 1880, *Young s.n.* (BM); Sund to Gagangar, Sept. 1880, *Young s.n.* (BM); Zanskar, Tetha, Tankse, 4000 m., *Koelz 5592* (US); Padri Pass to Bhadrar, *Schlagintweit 3067* (US); Wingle Nullah, *Pinfold 195* (BM); Banihal village, Kashmir-Jammu Road, 1800 m., *R. R. Stewart 12555* (GH); Apharwat, 3000–3500 m., *Timins 257* (BM); Aliabad, 3200 m., *Clarke 28725* (BM); Ladak: Hernes, 3700 m., *Koelz 2539* (GH, US); Hemis, *Koelz 6393* (MICH, US); Mulbekh, Robila, *Koelz 6157* (GH, MICH, US); Mitsahoi, 3000 m., *R. R. Stewart 12553* (GH); Dah, right side of Indus Valley, *Schlagintweit 1212* (GH); Marsho, *Koelz 6393a* (GH); Dras, 3000 m., 31 Aug. 1922, *R. R. Stewart s.n.* (K); Chitta Pani Valley, Poosiana, *Levinge* in *Clarke 27124* (BM). Miscellaneous: Himal. bor. occ., regio temp., 8000–10,000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM, GH-as *Cynoglossum* No. 6), 6–9000 ped., *Thomson s.n.* (BM, K, US-as *Cynoglossum denticulatum*).

3b. Var. **glochidiatum** (Wall. ex Benth.) Kazmi, comb. nov.

Cynoglossum glochidiatum Wall. ex Benth. in Royle, Illustr. Bot. Himal. Mount. 1: 306. 1839.

TYPE: Nepaulia, *Wallich 922* (K).

ICON.: Lindl. in Bot. Reg. *t. 15.* 1841.

Dorsal surface of the nutlets ovate, less sunken, covered usually with few vertical appendages along the more or less prominent longitudinal keel, apex obtuse to acutish, marginal appendages at their bases not at all, to slightly dilated, sometimes confluent, forming a narrow marginal wing.

West Pakistan: GILGIT AGENCY: Baltistan, Chalpani Nala, 3000–3500 m., *Duthie 13816* (K); Chutrun, 2000 m., *Ludlow 262* (BM). HAZARA DIST.: Kaghan Valley, Silan, 12 July 1899, *Inayat s.n.* (K); between Balakot and Babusar Pass, *Abel 128* (BM).

Kashmir: Vicinity of Sonamarg, on the Sind river, 50 road-miles east-northeast of Srinagar, 2000 m., *Dickason 107* (MICH, US), 2200 m., *Dickason 106* (MICH); Purig, Tangola, *Koelz 6075* (MICH, US); vicinity of Pahlgam, on east Lidder River, 27 road-miles north of Islamabad, *Dickason 111* (MICH); Pahlgam to Lake Tuliori, 2300 m., *R. R. Stewart 21848* (US).

4. **C. microglochin** Benth. in Royle, Illustr. Bot. Himal. Mount. 1: 305. 1839; A. DC. in DC. Prodr. 10: 151. 1846; C. B. Clarke in Hook. f. Fl. Brit. India 4: 158. 1883; Brand, Pflanzenr. IV. 252(Heft 78): 133. 1921.

TYPE: Kashmir, *Royle s.n.* (K?).

Perennial herb, erect, 35–90 cm. tall. Stems simple or branched, densely covered with white trichomes. Basal leaves petiolate, lanceolate to oblong-lanceolate, on both surfaces densely covered with soft white trichomes, attenuated at both ends, 6–20 cm. long including petioles, 12–30 mm. broad; cauline leaves sessile ovate to elliptic, acuminate, round towards the base, to 6 cm. long, 30 mm. broad, nerves sunken above, raised below, upper surface densely covered with thin, antrorsely subappressed to appressed, white trichomes 0.5–1 mm. long, arising from prominent white tuberculate bases, lower surfaces densely albido-tomentose; upper cauline leaves smaller in size. Inflorescence terminal or axillary, ebracteate, short in flower, later elongated to 15 cm., simple or geminate, branches arched out, bearing closely set flowers and to 10 mm. distant fruits. Pedicels none to 0.7 mm. long, reflexed. Calyx divided to 4/5 of its length, lobes ovate-elliptic, obtuse, erect, 3.5–4.5 mm. long, 1.5–2 mm. broad in flower, externally covered with antrorsely subappressed, unequal white trichomes, densely tomentose internally at the margins; spreading in fruit, sometimes slightly incurved at the margins, enlarged to 5.5–6.5 mm. long and 3–3.5 mm. broad. Corolla pale blue to light purple, campanulate, tube more or less equalling the limbs, ca. 3.5 mm. long, lobes ovate, spreading, 3.5 mm. long, ca. 2.5 mm. broad; faucal appendages emarginate, puberulous, ca. 1 mm. long, 0.7 mm. broad. Anthers ovate, 1.2–1.4 mm. long, 0.5 mm. broad; filaments short, inserted ca. 3 mm. above the corolla base. Nutlets ovate, puberulous to minutely and densely pubescent, 4.5–5.5 mm. long, 3–3.5 mm. broad, margins appendiculate, appendages 0.5–0.7 mm. long, distant, glochidiate at apex, dilated at base, usually confluent, forming a narrow, thick, marginal wing, dorsal middle area concave, sometimes with quite conspicuous longitudinal keel, with few scattered vertical glochidiate appendages, appendages on the lateral and ventral sides smaller than those of the margins. Style 3.5–5 mm. long; stigma capitate.

DISTRIBUTION: West Pakistan, Kashmir, northwest India.

West Pakistan: HAZARA DIST.: KAGHAN VALLEY: between Balakot and Babusar Pass, *Abel 135* (BM).
Kashmir: Pooniana (?), 3000 m., *Clarke 28819* (BM).

Very little material belonging to *Cynoglossum microglochin* is available in herbaria. The type collection by Royle from Kashmir is also not traceable. Bentham (*l. c.*), C. B. Clarke (*l. c.*) and Brand (*l. c.*) describe the basal leaves as attenuated towards the base, and differentiate this species from the closely allied *C. nervosum* by its fewer cauline leaves,

ovate to elliptic, and acute, densely pubescent above, pubescent below, whereas *C. nervosum* has oblong to elliptic cauline leaves, sparsely hirsute on both surfaces. From the specimens of both the species available to me, the differentiating characters seem to be quite stable. The two specimens cited above are immature and lack fruits, but they agree in the form of leaves, their indumentum, and in the floral parts with a very good and complete specimen collected from Dalhousie by C. B. Clarke (23 Sept. 1874, *Clarke 2298* at Kew) and determined by him, which agrees in all its details with Bentham's original description.

5. **C. nervosum** Benth. ex C. B. Clarke in Hook. f. Fl. Brit. India **4**: 158. 1883; Hook. Bot. Mag. **123**: *t. 1713*. 1897; Brand, Pflanzenr. IV. **252**(Heft 78): 142. 1921; Riedl in Rechinger, Fl. Iranica **48**: 146. 1967.

Omphalodes nervosa Edgeworth ex C. B. Clarke in Hook. f. Fl. Brit. India **4**: 158. 1883, *nomen nudum*.

TYPE: WESTERN HIMALAYA: Kulu, Jalauri Pass, *Edgeworth s.n.* (K).

ICON.: Hook. l. c. *t. 1713*. 1897.

Perennial erect herb, to 90 cm. tall. Stems solitary or few, branched above the base; stem and branches covered with crisped white, spreading trichomes, to 1.5 mm. long, arising from tuberculate bases on the lower part; with shorter, subappressed trichomes on the upper part. Basal leaves petiolate, petioles to 4 cm. long, lamina ovate to oblong-ovate, entire, rounded at apex, attenuated towards the base, to 4 cm. long and 1.5 cm. broad, covered on both surfaces with soft, white, crisped, spreading trichomes, usually arising from minute tuberculate bases; lower cauline leaves petiolate, petioles to 10 cm. long, lamina lanceolate, acute, gradually narrowed at base, to 12 cm. long and 2 cm. broad, indumentum like that of the basal leaves; middle and upper cauline leaves sessile, narrow to broadly lanceolate, to 7 cm. long, gradually reduced in size upwards. Inflorescence terminal or axillary, bifurcate, branches 2–3 cm. long, scorpioid in flower, later elongated to 10 cm., bearing 10–20 mm. distant fruits. Pedicels to 1 mm. long, in flower, sometimes elongated to 3 mm. and reflexed in fruit. Calyx divided to the base, lobes oblong-ovate, obtuse, sparsely to densely covered with long, soft, spreading trichomes, dorsally sometimes ciliate at the margins, more or less glabrous within, up to 3.5 mm. long and 1 mm. broad in flower. Spreading and enlarged to 4.5(–5) mm. long, 1.5 mm. broad in fruit. Corolla blue, infundibuliform, tube equalling or longer than the calyx, limbs 7–8 mm. in diameter, divided for 4/5 of its length, lobes transversely ovate, ca. 3 mm. long, 4 mm. broad, patent; faucal appendages emarginate, ciliate at the margins, puberulous above, 1 mm. long and broad. Anthers oblong-ovate, 1–1.5 mm. long; filaments 0.3 mm. long, inserted adjacent to the bases of the faucal appendages. Style to 3.5 mm. long, filiform, stigma capitate. Nutlets ovate, to 4.5 mm. long, 3 mm. broad, appendages

glochidiate, marginal ones dilated at their bases, confluent, forming a narrow or broad marginal wing, dorsal appendages few to many.

DISTRIBUTION: Afghanistan, West Pakistan, Kashmir, northwest India.

5a. Var. **nervosum**.

Petioles of the lower cauline leaves 3–4 cm. long; leaves covered on both surfaces with trichomes usually arising from prominent tuberculate bases; calyx lobes to 6 mm. long in fruit; fruiting pedicels usually shorter than the calyx; corolla 9–11 mm. in diameter.

Kashmir: above Tragbal, 3500 m., *Osmaston 13* (K); Hunan Nullah, Chamba Pangi, ca. 3000 m., *R. R. Stewart 2827* (K); Chamba, Aug. 1880, *Ellis 187, 405B* (K). Reported from: Gorai, *Meebold 4183*; Margan Pass, *Meebold 4182*.

5b. Var. **petiolatum** (Hook.) Kazmi, comb. nov.

Anchusa petiolata Hook. Bot. Mag. **67**: *t. 3858*. 1841.
Cynoglossum petiolatum (Hook.) A. DC. in DC. Prodr. **10**: 149. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 158. 1883; Brand, Pflanzenr. IV. **252** (Heft 78): 141. 1921.

TYPE: e Nepalia in hort. bot. Glascovium introduc.

ICON.: Hook. l. c. *t. 3856*. 1841.

Petioles of the lower cauline leaves 5–8 cm. long; leaves covered on both surfaces with soft trichomes usually not arising from prominent tuberculate bases; calyx lobes to 8 mm. long in fruit, fruiting pedicel usually longer than the calyx; corolla 16–18 mm. in diameter.

Kashmir: Bhujaz, foot of Umasi La, Zanskar Frontier, 3300 m., *Ludlow & Sherriff 9197* (BM). Reported from: alpine western Himalaya, Zanskar, near Umasi Pass, *Thomson s.n.* (K).

6. **C. stewartii** Kazmi, sp. nov.

TYPE: KASHMIR: Pahlgam to Lake Sorus, 10,000–11,000 ft., flowers dark blue purple, basal leaves large, 8 Aug. 1945, *R. R. Stewart 21584* (GH-holotype).

Herba perennis, erecta, ad 150 cm. alta. Caules brunneoli, striati, singulares vel numerosi, ad basim plerumque lignei (interdum lignei supra), simplices vel ramosi, rami longi, divaricati; caules ramique infra plerumque sparse pilosi, raro glabri, nitidi, supra plus minusve dense trichomatibus patentibus vel subappressis vestiti, trichomata ad 1 mm. longa. Folia basalia petiolata, petioli ad 18 cm. longi, lamina ovata vel ovato-lanceolata, integra, acuminata, ad basim plerumque truncata, interdum abrupte attenuata vel raro subcordata, manifeste nervata, ad 26 cm. longa, 12 cm. lata, supra uniformiter sparseque trichomatibus albis, tenuibus, patentibus vestita, trichomata ad 0.5 mm. longa, ad basim magni-tu-

berculata, infra trichomatibus densioribus, patentibus vel appressis, etuberculatis; foliis caulina petiolata, petioli ad 6 cm. longi, plerumque breviores, lamina ovato-lanceolata, acuminata, gradatim attenuata ad basim; folia caulina superiora sessilia vel subsessilia, in magnitudine sursum gradatim reducta. Inflorescentia terminalis vel axillaris, plerumque geminata, interdum dichotome ramosa, brevis, scorpioidea, in juventute flores approximati, deinde ad 15 cm. longa et fructibus distantibus ad 15 mm. Pedicelli ad anthesin perbreves; in fructu calycem aequantes, vel breviores vel interdum longiores. Calyx paene 4/5 divisus, lobi oblongo-ovati, obtusi, 3.5–4.5 mm. longi, 1.5–2 mm. lati ad anthesin, extus trichomatibus mollibus albis antrorse appressis vestiti, trichomata ad 0.5 mm. longa, intus densiore vestiti, trichomata breviora; lobi ad margines albido-tomentosi, in fructu ad 5 mm. longi et 3 mm. lati, patentes. Corolla purpureo-caerulea, infundibuliformi-campanulata vel rotata, tubus calycem aequans, 4–5 mm. longus, limbus ad basim divisus, lobi late ovati, patentes, 3–4 mm. longi, 3.5–4.5 mm. lati; appendices faucales trapeziformes, subemarginatae, puberulae. Antherae ovatae, 1.6 mm. longae, 0.7 mm. latae; filamenta perbrevia, supra basim ca. 3.5 mm. inserta. Nuculae late ovatae, ca. 4 mm. longae, 2.5 mm. latae, plus minusve acutae, bases rotundatae, margines appendiculatae, appendices ad 1.5 mm. longae, 0.5 mm. latae ad basim, apex glochidiatus, bases liberae vel subconfluentes cum ala angusta marginale, dorsum planum, glabrae vel interdum puberulae, longitudinaliter subcarinatae, 1–3 appendicibus verticalibus, appendices laterales et ventrales erectae, glochidiatae. Stylus 2.5 mm. longus, filiformis, stigma capitatum.

DISTRIBUTION: West Pakistan, Kashmir, northwest India.

West Pakistan: HAZARA DIST.: KAGHAN VALLEY: Kund Bangala, 2500 m., *Kazmi 2572* (PES); Bala Bhurj, 3000 m., *Inayat 19520* (K); Kamalban, 17 June 1899, *Inayat s.n.* (K), *Kazmi 2528a, 2532a* (PES); Silan, 12 July 1899, *Inayat s.n.* (K). RAWALPINDI DIST.: Murree Hills, along the pipeline from Murree north to Nathia gali, 2500–3000 m., *Dickason 109* (MICH). SWAT STATE: Bishigram, 3000 m., *R. R. Stewart & Rahman 24957* (BM); Bahrain, 2500 m., *Kazmi 2510* (PES); above Utror, 2500–3000 m., *R. R. Stewart & Rahman 25228* (BM).

Kashmir: Vicinity of Pahlgam, on east Lidder River, 27 road-miles north of Islamabad, *Dickason 108* (MICH); Pahlgam to Lake Sorus, 3000–3500 m., *R. R. Stewart 21584* (GH-type); Pahlgam, *R. R. Stewart 8319, 21723a* (GH), 2500 m., *R. R. Stewart 21504* (GH, K); Ferozpur Nullah near Gulmarg, 3000 m., *R. R. Stewart 12963* (GH); Sonamarg, *R. R. Stewart 6354, 7198 1/2* (K), 3000 m., *R. R. Stewart 12960* (GH); Chinari, *Kazmi 241* (PES); Gulbarg, 2700 m., *R. R. Stewart 12961* (GH); Jhelum Valley, Tilpatra forests, near Rampur, *Ludlow & Sherriff 7714* (GH); SIND VALLEY: Gangangir, hill face, *Ludlow & Sherriff 7970* (BM); Gund, 2000 m., *Ludlow & Sherriff 7695* (BM); Kishanganga Valley, Sharda, *R. R. & I. D. Stewart 17769* (MICH). Miscellaneous: Himal. bor. occ., 6000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM).

The specimens cited above are mostly named as *C. nervosum* or *C. microglochin* in herbaria, but they are very different from both these

species and deserve specific recognition based on the following distinguishing characters.

Cynoglossum stewartii is a tall perennial, taller than either of the species cited above; its basal leaves are very large, petiolate with petioles to 18 cm. long; lamina ovate to ovate lanceolate, truncate at base, abruptly narrowed or rarely subcordate, to 20 cm. long and 12 cm. broad. In the other two species petioles and lamina of the basal leaves never exceed 10 cm. and 12 cm. in length, respectively. In shape the lamina are ovate to oblong-ovate and always gradually narrowed towards the base. The middle and upper cauline leaves in *C. stewartii* are distinctly petiolate, with petioles sometimes to 6 cm. long, and the uppermost leaves subsessile to rarely sessile, these are gradually narrowed towards the petioles at base. In *C. nervosum* and *C. microglochin* the middle cauline leaves are sessile to subsessile and the upper ones distinctly sessile. In *C. nervosum* the upper cauline leaves are more or less narrowed, but in *C. microglochin* these are obviously rounded at base. The trichomes on both surfaces of the leaves of *C. stewartii* do not exceed 0.5 mm. in length, whereas in both the other species they are 0.5–1 mm. long. In form of the calyx and corolla, *C. stewartii* closely resembles *C. microglochin*, excepting for some minor details given in the descriptions.

Species not seen

C. schlagintweitii (Brand) Kazmi, comb. nov.

Adelocaryum Schlagintweitii Brand, Repert. Sp. Nov. **13**: 548. 1915; Pflanzenr. IV. **252** (Heft 78): 78. 1921.

Type: Tibet: Provinz Dras: Kargil, zwischen Suru und Tsringmat, *Schlagintweit 7211* (Breslau).

Perennial subshrubby herb, covered all over with short trichomes arising from tuberculate bases. Basal leaves petiolate, oblong to lanceolate, (including the petioles) 5–6 cm. long, 5–8 mm. broad, obtuse, attenuate towards the base; lower cauline leaves short petiolate, the upper sessile, much reduced. Inflorescence long, lax, many flowered. Calyx lobes oblong, obtuse, pilose. Corolla campanulate, 3 mm. long, lobes broadly ovate, tube short; faucal appendages broader than long, semilunar. Stamens inserted on the lower part of the corolla tube, filaments short. Style nearly half the length of the calyx. Nutlets (usually two abortive) ovoid, 4 mm. long, appendiculate at the margins, appendages glochidiate at apex, dorsally carinate, the ventral scar very small.

Distribution: Kashmir, southwest Tibet.

Kashmir: Kargil, between Suru and Tsringmat, *Schlagintweit 7211* (Breslau).

C. flexuosum (Brand) Kazmi, comb. nov.

Adelocaryum flexuosum Brand, Repert. Sp. Nov. **14**: 145. 1915; Pflanzenr. IV. **252** (Heft 78): 78. 1921.

TYPE: KASHMIR: Gurez (nortlich von Srinagar, der Haupt Stadt von Kaschmir), 3 und 4. 10. 1856, *Schlagintweit 7612* (Breslau).

Annual (?) herb, stems delicate, flexuous, to 30 cm. or longer, covered with spreading trichomes. Basal leaves not seen; cauline leaves short petiolate, the upper sessile, oblong to lanceolate, 3–4 cm. long, 10–16 mm. broad, attenuate at both ends. Inflorescence terminal, lax, many flowered. Pedicels of the lower fruits longer than the calyx. Calyx lobes oblong-elliptic, obtuse, to 3 mm. long. Corolla cylindric-campanulate 4.5 mm. long, tube equalling the limb; faucal appendages subquadrate, apex emarginate. Stamens inserted at the middle of the corolla tube, anthers reaching the bases of faucal appendages, filaments short. Style equal or subequal to the calyx. Nutlets 3 mm. long, dorsally appendiculate, appendages glochidiate at apex.

DISTRIBUTION: West Pakistan.

West Pakistan: GILGIT AGENCY: Gurez, *Schlagintweit, 7612* (Breslau).

Since I did not see the types of the two species cited above, the descriptions given here are according to Brand (l. c.). From the descriptions the taxa appear to belong to the genus *Cynoglossum*, and the species to be closely related to *C. wallichii*. On examination of the original material the species may, however, prove to be the same as or varieties of *C. wallichii* or *C. lanceolatum*.

26. **Actinocarya** Benth. in Benth. et Hook. f. Gen. Pl. 2: 846. 1876.

TYPE SPECIES: *A. tibetica* Benth.

Slender procumbent or diffuse annual herbs, sparsely strigose or nearly glabrous. Leaves alternate. Flowers minute, solitary on axillary pedicels. Calyx divided to the base, 5-lobed, hardly enlarged in fruit. Corolla campanulate, lobes broad-ovate, slightly shorter than the tube, obtuse, spreading, imbricate in bud; faucal appendages 5, very small, transversely linear. Stamens 5, inserted in the lower part of the corolla tube, anthers included, small, ovate, obtuse; filaments short. Ovary deeply 4–lobed; style short, stigma small. Nutlets 4, obovoid-oblong, appendiculate, appendages glochidiate at apex, free or dilated at base, confluent, forming marginal wings or a coniform dorsal crest, attached apically or subapically to a plane gynobase, turgid at the margins.

Species 2, distributed in Kashmir, southwest Tibet and northwest India.

KEY TO THE SPECIES

a. Leaves glabrous on the upper surface, with few short trichomes below; sepals bearing scattered short trichomes externally; fruits densely covered with minute, frequently uncinate trichomes and scattered appendages. . . . . 1. *A. tibetica*.

a. Leaves with long trichomes on both surfaces and at the margins; sepals bear-

ing few scattered trichomes externally, ciliate at the margins; fruits glabrous, appendiculate, appendages forming a dorsal crest. . . . . 2. *A. acaulis*.

1. **A. tibetica** Benth. in Benth. & Hook. f. Gen. Pl. 2: 846. 1876; C. B. Clarke in Hook. f. Fl. Brit. India 4: 154. 1883; Gürke in Nat. Pflanzenfam. IV. 3a: 101. 1893; Brand, Pflanzenr. IV. 252(Heft 78): 162. 1921.

TYPE: WEST TIBET: Nubra, alt. 13,000 ft., near Karsar village, *Thomson s.n.* (K-holotype, GH-isotype).

ICON.: Hooker, Icon. 23: *t. 2256.* 1893.

Annual, decumbent or erect herb, to 15 cm. tall. Stem solitary or many, slender, weak, unbranched, usually glabrous in the lower parts, with few scattered, spreading, minute, trichomes above. Basal leaves few, obovate-spathulate, entire, sometimes slightly revolute at margins, apex round, narrowed towards the base into long petioles, (including petioles) to 25 mm. long, 1.5–5 mm. broad, glabrous on both surfaces, or the lower surface bearing few scattered, retrorsely subappressed minute trichomes arising from tuberculate bases; cauline leaves usually with shorter petioles. Flowers axillary throughout the length of the plant. Pedicels short, in flower erect in the axils of the lower leaves, up to 25 mm. long in fruit, slender, with antrorsely suberect minute trichomes, gradually reduced in size upwards. Calyx divided to the base, lobes lanceolate to broad-lanceolate, obtuse to subacute, externally sparsely pilose, ca. 1.5 mm. long, 0.5 mm. broad in flower; erect, not at all to slightly enlarged in fruit. Corolla light blue, campanulate, tube usually shorter than the calyx, ca. 1 mm. long, limb equalling or slightly longer than the tube, divided nearly to the base, lobes broad-ovate, ca. 1 mm. long and broad, spreading; faucal appendages very small. Stamens 5, anthers small, ovate, obtuse, included, filaments short. Ovary 4-lobed, style short, stigma small, capitate. Nutlets 4, grayish, obovoid-oblong, divaricate, ca. 2 mm. long, bearing numerous minute, frequently uncinate trichomes as well as numerous appendages, appendages glochidiate at apex, 1–1.5 mm. long, scattered, not forming a dorsal crest.

DISTRIBUTION: West Tibet, Kashmir, northwest India (?).

Kashmir: Nubra near Karsar village, *Thomson s.n.* (K, GH); **Ladakh:** Nanu, 4500 m., *Koelz 2358* (GH); Henus, 3300 m., *Koelz 2558* (GH). Reported from: Kambajong, *Prain s.n.* (in Herb. Bornmüller); without locality, *King's* collector, *1882* (DD).

2. **A. acaulis** (W. W. Smith) I. M. Johnston, Jour. Arnold Arb. 21: 53. 1940.

Eritrichium acaule W. W. Smith, Rec. Bot. Surv. India 4: 225. 1911.

TYPE: Naku La, Llonakh, Sikkim, top of Pass, 17,500 ft., 3 Aug. 1909, *Smith & Cave 2811* (CAL-holotype, GH-, K-isotypes).

Annual prostrate compact herb, sometimes branched near the base; branches many, very short, fleshy, covered with many scattered, spreading trichomes to 0.5 mm. long, arising from tuberculate bases. Leaves obovate-spathulate, entire, rarely slightly revolute at the margins, apex round, narrowed at base into long, usually winged petioles ± dilated below, (including petioles) to 20 mm. long and 4 mm. broad, bearing on both surfaces and margins crisped, spreading trichomes, to 0.7 mm. long arising from tuberculate bases; cauline leaves, if any, shorter. Flowers solitary in the axils of leaves or sometimes few axillary and congested on the top of the short branches. Pedicels short in flower, to 10 mm. long, fleshy, in fruit bearing many spreading trichomes. Calyx divided nearly to the base, ca. 1.5 mm. long in flower, lobes erect, ovate to oblong, obtuse to subacute at apex, bearing few scattered trichomes dorsally, with ciliate margins, enlarged to 2 mm. long and ± 1 mm. broad in fruit. Corolla blue, campanulate, tube usually equalling the calyx, limbs shorter than the tube, divided to the base, lobes rotundate, spreading; faucal appendages very small. Stamens 5, included, anthers ovate, small, filaments short. Nutlets 4, ovoid-oblong, glabrous, appendiculate, appendages to 1 mm. long, glochidiate at apex, dilated at base, confluent and forming a dorsal crown.

DISTRIBUTION: Kashmir, northwest India, Sikkim.

Kashmir: LADAKH: Rupshu, Kiangchu, Lachulung, 4500 m., *Koelz 6650* (GH). Reported from: Rupshu, Purga, *Koelz 2184*; Nanu, *Koelz 2358*.

Both species of *Actinocarya*, widely distributed in the Himalayas, are very similar in gross habit. *A. tibetica* is apparently glabrous though the leaves are pustulate and strigose beneath. The dimorphic fruits bear numerous minute, frequently uncinate trichomes. In *A. acaulis* the stem and the leaves bear relatively coarse, elongate, loosely appressed hairs. The fruit is nearly glabrous and the secondary glochidiate appendages are fewer, tending to be crowded just outside the coarse dorsal margin of the nutlet.

The fruits of *A. tibetica* are dimorphic. Those borne along the stems are long pedicellate and composed of apically attached nutlets bearing a small crown on the back towards the base. Outside this small crown are numerous scattered glochidiate appendages. The fruits produced about the base of the plant have short stout pedicels and more compressed nutlets. The dorsal crown is incomplete on these, or entirely absent. Numerous scattered glochidiate appendages, are however, always present.

27. **Lithospermum** L. Sp. Pl. 132. 1753; Gen. Pl. ed. 5. 64. 1754.

Buglossoides Moench, Meth. 418. 1794; I. M. Johnston, Jour. Arnold Arb. **38:** 38. 1954.

TYPE SPECIES: *L. officinale* L. (Lectotype species).

Annual or perennial, erect or decumbent, hispid or rough herbs. Leaves

alternate. Flowers white, blue or yellow, axillary and solitary or in terminal bracteate racemes. Calyx divided to or nearly to the base, usually enlarged in fruit. Corolla infundibuliform to hypocrateriform, either longitudinally plicate or gibbous at throat, lobes imbricate in bud, later suberect to spreading. Stamens 5, included; anthers oblong, obtuse or apiculate; pollen encircled with a single row of 6 to 9 pores. Ovary deeply 4-lobed; style usually filiform, stigma bifid. Nutlets 4, erect, ovoid, stony, smooth, rough or tuberculate, attached by a basal scar to the nearly flat gynobase.

A polymorphous genus of 50 to 60 species, distributed mainly in America. About 10 species are known in Africa and about 10 in Europe and Asia, including three species from West Pakistan and Kashmir.

KEY TO THE SPECIES

a. Nutlets shining, white, smooth. ..... 3. *L. officinale.*
a. Nutlets rough, grayish, tuberculate.
  b. Plants weak, usually little branched; nutlets weakly attached by a narrow areola to the gynobase. ..... 1. *L. arvensis.*
  b. Plants robust, usually much branched; nutlets firmly attached by a broad areola to the gynobase. ..... 2. *L. tenuiflorum.*

1. **L. arvenis** L. Sp. Pl. 132. 1753; Ledeb. Fl. Rossica **3**: 129. 1847; Boiss. Fl. Orient. **4**: 216. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 174. 1883; M. Pop. Fl. URSS **19**: 165. 1953; Riedl in Rechinger, Fl. Iranica **48**: 151. 1967.

Margarospermum arvense Decne. in Jacquem. Voy. Inde Bot. 122. 1844.

TYPE: "Habitat in Europae agris et arvis," Herb. No. 181.4 (LINN).

ICON.: Hegi, Illustr. Fl. Mitt. Eur. **5**(3): *fig. 3112, a–c.* 1927.

Annual, erect herb to 50 cm. tall. Stems slender, usually solitary, rarely few, little branched, covered with antrorsely appressed, white trichomes with tuberculate bases. Basal leaves few, ovate, entire, roundish, gradually or abruptly narrowed into long petioles, (including petioles) to 20 mm. long and 5 mm. broad, covered on both surfaces with minute subappressed trichomes arising from tuberculate bases; lower cauline leaves similar to the basal ones; middle cauline leaves oblong, oblong-ovate or lanceolate, subsessile or with very short petioles; upper cauline leaves, subsessile to sessile, lanceolate, obtuse to subacute. Inflorescence of terminal racemes, short in flower, elongated in fruit, bracteate, bracts leaf-like. Pedicels lacking in flowers, stout, pubescent, to 3 mm. long in fruit. Calyx divided nearly to the base, lobes linear, acute, to 6 mm. long and 0.5 mm. broad, densely covered with spreading, stiff white trichomes with tuberculate bases, enlarged to 8 mm. long and 1.5 mm. broad, connate at the base and forming a cup to hold the nutlets in fruit. Corolla white to light blue, tubular-infundibuliform, externally minutely strigose, corolla tube longitudinally pli-

cate from the top of the anthers to the throat, glandular or minutely hairy, 4–5 mm. long, lobes ovate, spreading, to 1 mm. long. Anthers oblong, apiculate, roundish at the base, to 1 mm. long; filaments very short, inserted 1–1.5 mm. above the corolla base. Nutlets 4, gray, pink, or light brown, ovate, usually abruptly narrowed in the upper half, tuberculate all over the surface, 3 mm. long, 2 mm. broad; areola basal, small.

DISTRIBUTION: Europe to Japan.

West Pakistan: CHITRAL STATE: Oihor Gol, 3000 m., *Bowes Lyon 841* (BM); Brumboret Gol, N. of Drosh, *Stainton 2226* (BM). HAZARA DIST.: Abbottabad, 1300 m., *R. R. Stewart 13690A* (GH, US). KHYBER AGENCY: Khyber Pass, 1100 m., *H. H. Johnston 143* (E); Forsapper, Khyber Pass, 1700 m., *H. H. Johnston 61* (E). QUETTA DIST.: Environ de Quetta, *Schmid 1572* (G). RAWALPINDI DIST.: Dhamyal near Rawalpindi, 500 m., *R. R. Stewart 19389A* (GH); Topi Park, Rawalpindi, *Pinfold 10* (BM); Murree Hills, Ghora Gali, 1700 m., field weed, *R. R. Stewart 12951* (GH).

Kashmir: Srinagar, 1700 m., *R. R. Stewart 12952* (GH); near Srinagar, *R. R. Stewart 63* (BM). Miscellaneous: Himal. bor. occ., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH).

2. **L. tenuiflorum** L. f. Suppl. 130. 1781; DC. Prodr. **10**: 75. 1846; Boiss. Fl. Orient. **4**: 217. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 175. 1883; M. Pop. Fl. URSS **19**: 164. 1953; Riedl in Rechinger, Fl. Iranica **48**: 150. 1967.

Myosotis tenuiflora Viviani, Fl. Libycae, 9. 1824.

TYPE: "Habitat in Aegypto," *Latourette*, Herb. No. 181.13 (LINN).

ICON.: Jacq. Icon. Pl. Rar. **2**: *t. 313*. 1793; Viviani, l. c. *t. 1. fig. 2*. 1824.

Very similar to *Lithospermum arvensis* except that the plants are robust; stems decumbent, many, usually branched, to 30 cm. long; leaves larger, cauline leaves usually sessile with a broad base; corolla 5–6 mm. long; areola of the nutlets broad and firmly attached to the gynobase.

DISTRIBUTION: North Africa and southeastern Europe to Central Asia, Afghanistan, West Pakistan, Kashmir, northwest India.

West Pakistan: CHITRAL STATE: Chitral village, 1500 m., *Stainton 2156* (BM). DIR STATE: Dir, *Salim 1* (K). HAZARA DIST.: Abbottabad, 1300 m., *R. R. Stewart 13691* (GH). KALAT DIST.: Surab to Kalat, ca. 20 km. from Surab, 1800 m., *Lamond 671* (E), *Rechinger 28327* (G, W). KHYBER AGENCY: Jamrud, 7.3.1898, *Duthie* (K). PESHAWAR DIST.: Islamia College, ca. 350 m., *Kazmi 2528* (PES); between Peshawar and Tarnab Farm, ca. 350 m., *Kazmi 2481* (PES); Pabbhi-Nowshehra, *Kazmi 2470* (PES); Peshawar, ca. 350 m., *Kazmi 21b* (PES), *Vicary s.n.* (K). QUETTA DIST.: Near Sanjawi, road from Harnai, 1500 m., *Lamond 1318* (E); Quetta, *Duthie 8680* (BM). RAWALPINDI DIST.: Rawalpindi, *Aitchison 1079* (K), *R. R. Stewart 1509* (K), *Kazmi s.n.* (PES). SWAT STATE: without locality, *Jafri s.n.* (E).

Kashmir: Kotli, ca. 900 m., *R. R. Stewart 27385* (GH); near Srinagar, *Duthie*

10841 (K); Tangmarg, 2200 m., *R. R. Stewart 12953* (GH). Miscellaneous: Himal. bor. occ., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM, GH), dated 4. 4. 1848 (K).

3. **L. officinale** L. Sp. Pl. 132. 1753; Ledeb. Fl. Rossica **3**: 130. 1847; Boiss. Fl. Orient. **4**: 218. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 175. 1875; M. Pop. Fl. URSS **19**: 162. 1953; Riedl in Rechinger, Fl. Iranica **48**: 149. 1967.

Margarospermum officinale (L.) Decne. in Jacquem. Voy. Inde Bot. 122. 1844. [This reference given in Index Kewensis, but the combination was not properly made by Decaisne.]

TYPE: "Habitat in Europae ruderatis," Herb. No. 181.1 (LINN).

ICON.: Reichenb. Icon. Fl. Germ. **18**: *t. 112. I, 1–4.* 1858; Hegi, Fl. Mitt.-Eur. **5**(3): *fig. 3115, a–f* and *3116.* 1927.

Erect perennial herb, to 100 cm. tall. Stems solitary or many, branched, branches to 20 cm. long; stem and branches covered with subappressed to patent trichomes, to 1.5 mm. long, arising from minute or large tuberculate bases. Leaves lanceolate, entire, sometimes slightly revolute, acute, to 8 cm. long, 20 mm. broad, covered with thin or thick, antrorsely subappressed trichomes with tuberculate bases, to 1 mm. long. Inflorescence bracteate, bracts leaflike. Pedicels very short in flower, erect, pubescent, elongate, to 4(–5) mm. long in fruit. Calyx divided to the base, lobes narrowly lanceolate, 3–4 mm. long in flower, not much enlarged, pubescent, trichomes spreading in fruit. Corolla yellowish, greenish or sometimes nearly white, hypocrateriform, 4–6 mm. long, corolla tube usually equalling, sometimes slightly longer or shorter than the calyx, 2.5–3.5(–4) mm. long, limb 4 mm. in diameter, lobes spreading, 1–1.5 mm. long, corolla throat with 5 trapeziform, intruded, distinctly invaginated appendages, densely velvety at apex, glanduliferous (especially on the sides). Filaments inserted at the middle of the corolla tube. Style 1–2 mm. long; stigmas 2, small. Nutlets ovate, white, smooth, shining, 3–4 mm. long.

DISTRIBUTION OF SPECIES: From Europe to central Asia.

The plants from Afghanistan, West Pakistan, and Kashmir are different from the specimens of *Lithospermum officinale* collected from the other areas of its distribution in having longer, stouter, and spreading trichomes on the stems. They are distinguished here as a variety.

Var. **stewartii** Kazmi, var. nov.

TYPE: KASHMIR: Banehal Pass, 9000 ft., July 1–4, 1931, *R. R. Stewart 12182* (GH-holotype).

A varietate *officinali* differt caulibus hispidulis, pilis gracilibus, rectis, divaricatis donatis.

DISTRIBUTION OF VARIETY: Afghanistan, West Pakistan, and Kashmir.

West Pakistan: KURRAM AGENCY: Kurram Valley, *Aitchison 338* (GH).
Kashmir: Banehal Pass, *R. R. Stewart 12182* (GH-type); Sind Valley, Gandarbal, 1800 m., *Ludlow & Sherriff 7621* (BM); Tilal Valley to Chorwan, ca. 3000 m., *R. R. & I. D. Stewart 18599* (GH); vicinity of Sonamarg, on the Sind River, 50 road-miles east-northeast of Srinagar, *Dickason 89* (MICH); Srinagar, *C. B. Clarke 29100A* (BM). Miscellaneous: Kashmir, *Kohli 1* (K); Himal. bor. occ., 6000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM, GH).

The new variety closely resembles *Lithospermum erythrorhizon* Sieb. & Zucc. (Abh. Bayer. Akad. Wiss. 4(3): 149. 1846) from eastern Asia in having spreading trichomes on the stem. In characters of the calyx and corolla, however, the plants of var. *stewartii* agree with typical *Lithospermum officinale*. In *L. erythrorhizon*, unlike the condition in *L. officinale*, the corolla limb is spreading and formed of rounded, equally long and broad corolla lobes, in diameter it is commonly equal to the total length (5–9 mm.) of the corolla. The fruiting calyx is usually 5–10 mm. long and several times longer than the nutlets.

28. **Arnebia** Forssk. Fl. Aegypt.-Arab. 62. 1775.

TYPE SPECIES: *Arnebia tetrastigma* Forssk.

Annual to perennial, erect to decumbent hispid herbs. Stems single to many, branched or unbranched, arising from a tap root. Inflorescence usually terminal, simple or forked, of scorpioid cymes, bracteate. Calyx divided nearly to the base, lobes accrescent, usually shorter than the corolla tube. Corolla regular or nearly so, yellow, cream, blue, or purple, sometimes with conspicuously spotted limb, salverform or rarely tubular, lobes strongly imbricate in bud, usually spreading or widely ascending, entire to sometimes lacerate, throat usually glabrous within, faucal appendages lacking. Anthers oblong to narrowly oblong, included to slightly exserted; filaments usually much shorter than the anthers, inserted at or below the throat of the corolla tube, at the same or different levels. Flowers heterostylic. Style slender, simple or simply forked or bifid, included to slightly exserted; stigmas 2–4, capitate, oblong or flabellate, simple or slightly bilobed. Usually one to four nutlets developing, these conic-ovoid, pyramidal or lance-ovoid, usually broadest at base, rough, tuberculate, verrucose, rugose or rugulose, surface usually dull; venter usually angulate, keeled, attachment basal, large, horizontal or suboblique. Gynobase flat or broadly pyramidal, attachment surface separated by lineal grooves, plane or somewhat concave.

Species 20 to 22, distributed from North Africa to Central Asia and the Himalayas.

KEY TO THE SPECIES

a. Plants distinctly perennial; corolla tube without annulus at base.
  b. Leaves with midrib only; inflorescence globose or broader than long.

c. Plants gray or silvery, stem arising from the center of the basal leaf-cluster, less than 15 cm. tall, leaves less than 5 mm. broad, herbage not glanduliferous. ..... 4. *A. inconspicua.*

c. Plants green or somewhat tawny, stem lateral to the basal leaf-cluster, usually 40 cm. tall, leaves usually 5–10 mm. broad, herbage usually glanduliferous. ..... 3. *A. euchroma.*

b. Leaves usually with 3–5 longitudinal ribs; inflorescence thyrsoid, evidently much longer than broad.

d. Thyrse continuous, with numerous exserted bracts; calyx lobes very slender and flexible. ..... 1. *A. benthamii.*

d. Thyrse interrupted, only the lowermost bracts protruding; calyx lobes slender, stiff. ..... 2. *A. speciosa.*

a. Plants annual to perennial; corolla tube with distinct annulus at base.

e. Plants flowering in the first year, but becoming perennial. . . 7. *A. guttata.*

e. Plants always annual.

f. Style bifid at apex to once again somewhat bifid; stigma deeply bilobed.

g. Corolla 20–35 mm. long, limb 10–15 mm. in diameter, lobes spreading, bearing distinct large dark purple patches; nutlets to 2 mm. long. ..... 11. *A. grandiflora.*

g. Corolla 12–18 mm. long, limb less than 10 mm. in diameter, lobes ascending, erect or slightly recurved, large purple patches lacking; nutlets 2–3.5 mm. long.

h. Corolla lobes ascending; calyx 4–5 mm. long in flower, 10–15 mm. long, hardened, connate and with very prominent midribs in fruit; nutlets 2–2.5 mm. long. .... 10. *A. decumbens.*

h. Corolla lobes erect to slightly recurved; calyx 8–12 mm. long in flower; 18–20 mm. long, hardened, connate and without prominent midrib; nutlets 3–3.5 mm. long. . 13. *A. simulatrix.*

f. Style once bifid at apex and stigma entire, or style undivided and stigma bilobed.

i. Corolla brown to dark purple, hardly exceeding the calyx. . . . . 12. *A. waziristanica.*

i. Corolla yellowish white, yellow or orange, sometimes with dark purple spots, never brown to dark purple, usually exceeding the calyx.

j. Corolla lobes at the margins undulate, crenate to fimbriate. . . . . 8. *A. fimbriopetala.*

j. Corolla lobes always entire.

k. Calyx lobes obtuse, 6–10 mm. long, 1–1.5(–2) mm. broad at base, in flower hardened with prominent midrib and marginal veins, elongated to 22 mm., dilated at base to 3–5 mm. in fruit. ..... 9. *A. linearifolium.*

k. Calyx lobes acute, 7–9 mm. long, 0.5–1.5 mm. broad at the base, in flower not hardened, with midrib not very prominent and veins invisible, elongated to 15 mm., hardly dilated at the base (to 2 mm.) in fruit.

l. Plants densely covered with stout trichomes; corolla yellow, 10–15 mm. long, villulose in a band ca. 1 mm. broad inside, limb 4–8 mm. broad; calyx lobes slightly unequal, to 7 mm. long, 1.5 mm. broad in flower, not much enlarged in fruit. ..... 5. *A. hispidissima.*

1. Plants loosely covered with slender trichomes; corolla yellow to orange, 20–23(–30) mm. long, glabrous inside, limb 10–15(–20) mm. broad, with 5 dark purple spots; calyx lobes equal, to 9 mm. long and 0.5 mm. broad in flower, enlarged in fruit to 15 mm. long and 1.5 mm. broad. ..... 6. *A. griffithii.*

1. **A. benthamii** (Wall. ex G. Don) I. M. Johnston, Jour. Arnold Arb. **35**: 56. 1954.

Echium benthamii Wall. Cat. No. 931. 1829, *nomen nudum*; G. Don, Gen. Syst. **4**: 333. 1838.
Macrotomia benthamii (Wall.) A. DC. in DC. Prodr. **10**: 27. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 177. 1883.
Leptanthe macrostachya Klotzsch in Reise Prinz Waldem. Bot. 95. *t. 63.* 1862.
Lithospermum benthamii (Wall. ex G. Don) I. M. Johnston, Jour. Arnold Arb. **33**: 333. 1952.

Type: India: Budrinath, *Wallich 931* (K-holotype, A-isotype).

Icon.: Hook. Bot. Mag. **114**: *t. 7003.* 1888; Coventry, Wild Flowers of Kashmir **1**: *t. 37.* 1923; Blatter, Beautiful Flowers of Kashmir **2**: *t. 45.* 1929.

Erect perennial herb with thick roots rich in purple dye, sometimes to 3 cm. in diameter. Stem solitary, fistulous, unbranched, arising from the center of the basal leaf-cluster, to 90 cm. long, densely covered with white, spreading trichomes tuberculate at base, to 3 mm. long. Basal leaves many, lanceolate, entire, acute, attenuated at both ends, with 3–5 prominent, longitudinally parallel ribs, to 30 cm. long and 3.5 cm. broad, covered on both surfaces with silvery, thin, spreading to subappressed trichomes, to 2 mm. long, arising from tuberculate bases; middle and upper cauline leaves gradually reduced in size upwards. Inflorescence a dense cylindrical thyrse, to 35 cm. long, 5–7 cm. thick at maturity; bracts linear-lanceolate, acuminate, densely hairy, exceeding the calyx, to 5 cm. long, 1.5–2.5 mm. broad. Calyx divided to the base, lobes linear-lanceolate, slender, acuminate, flexible, densely pubescent, 13–25 mm. long in flower, 25–35 mm. long in fruit. Corolla pink or purple to maroon, usually shorter than the calyx, 20–25 mm. long, tube gradually expanding after 10–12 mm. to form a 4–5 mm. long, 5–7 mm. wide throat lacking glands or appendages, lobes ovate, 2.5–3.5 mm. long, 2–3 mm. broad. Anthers borne at the middle of corolla tube, sometimes partially exserted at its summit, 2–2.5 mm. long. Style reaching the middle of the corolla tube or to the summit, entire or very inconspicuously forked at apex; stigmas 2, broader than long, more or less separate. Nutlets broadest near the middle, narrowed towards the basal attachment, 3–4 mm. long, irregularly rugose and somewhat tuberculate, surface dull from abundant very minute papillae, ventral keel continuous over the beaked apex, attachment scar frequently with two distinct dorsal traces.

DISTRIBUTION: West Pakistan, Kashmir, north and northwestern India to Nepal.

West Pakistan: GILGIT AGENCY: Deosai Plains, *Osmaston 86* (K); HAZARA DIST.: Kaghan valley, Makra Hill, beyond Shogran, 3500 m., *Kazmi 634* (PES); Paya, between Shogran and Makra, 3000 m., *Kazmi 2571* (PES); Naran, on the top of Ganji Pahari, ca. 3000 m., *Kazmi 2266b* (PES); Saiful Maluk, 3000 m., *Shaukat Ali 128* (BM, RAW), *Kazmi 2278b* (PES); Batakundi, valley towards the east of the Rest House, ca. 3000 m., *Kazmi 2571* (PES); Siran Valley, north of Shahid Pani Rest House, on the slopes of Musa ka Musalah, 3000 m., *Kazmi 839b* (PES); on the eastern slope of Musa ka Musalah, near the top, 3500 m., *Kazmi 459a* (PES); Nathiagali Hills, Miran Jani, near the top, 3500 m., *Kazmi 326b* (PES). SWAT STATE: Swat Kohistan, ca. 3000 m., *Kazmi s.n.* (PES). Reported from Kagan, Makra, *Inayat 21999* (?).

Kashmir: Above Gulmarg, ca. 3000 m., *Duthie 11323* (BM, E); Pangtran to Thanin, 1884, *Young s.n.* (BM); Near Sinthan Pass, head of Bringhi Valley, *Ludlow & Sherriff 8183* (BM); Sind Valley, Zaiwan, 3000–4000 m., *Ludlow & Sherriff 2661* (GH); Masjid Gali, ca. 4000 m., *R. R. & I. D. Stewart 18429* (GH); Aliabad, ca. 3000 m., *C. B. Clarke 28909* (BM); Kalohoi Valley Pass, 4000 m., *Polunin 56/539* (BM, E). Miscellaneous: in Herb. late East India Co., *Falconer s.n.* (GH); Himal, bor. occ., 10,000–12,000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH); Kashmir, 3200 m., *Mrs. Prescott-Decie* (1915) *s.n.* (BM); Kashmir, ca. 3100 m., *R. R. Stewart 21805* (GH).

2. **A. speciosa** Aitch. & Hemsl. Jour. Linn. Soc. Bot. **18**: 81. 1881 and **19**: 179. 1882; Riedl in Rechinger, Fl. Iranica **48**: 168. 1967.

Lithospermum speciosum (Aitch. & Hemsl.) I. M. Johnston, Jour. Arnold Arb. **34**: 13. 1953.

Macrotomia speciosa (Aitch. & Hemsl.) Kitamura, Fl. Afghanistan 322. 1960.

TYPE: PAKISTAN: Hills behind Kaiwas, Kurram Valley, 9000–12,000 ft., open grassy spots, 3 July 1879, *Aitchison 720* (K-holotype).

ICON.: Aitch. & Hemsl. l. c. **19**: *t. 24*. 1882.

Erect perennial herb. Stems simple, arising from the center of the basal leaf-cluster, to 60 cm. long, 8 mm. thick at the base, covered with stout, white trichomes retrorsely appressed on the lower part of the stem, spreading on the upper part, 2–4 mm. long. Basal leaves narrowed above the broad, sheathing, dye-stained base, broadest above the middle, and then gradually narrowed to an acute apex, 10–15(–25) cm. long (*fide* Aitch. & Hemsl.), 7–10 mm. broad; lower cauline leaves similar to the basal ones, with three strong, longitudinal ribs, covered on both surfaces with slender stiff, spreading to ascending, sometimes retrorse trichomes, 1–2(–3) mm. long, those on the upper surface arising from minute tuberculate bases; middle cauline leaves lanceolate, 5–14 cm. long, 5–8 mm. broad near the base; upper cauline leaves gradually reduced upwards. Inflorescence an elongate interrupted cylindrical thyrse, 15–25 cm. long, 5–7 cm. thick, composed of small terminal cymes borne in the leaf axils along the upper half of the stem; cymes densely flowered, at first glomerate and 3–5 cm.

broad, but in age tending to elongate and become obviously scorpioid; bracts shorter than the calyces, subtending leaves surpassing only the lower cymes. Calyx hispid, 17–18 mm. long in flower, elongated to 21 mm. in fruit; lobes equalling to slightly surpassing the corolla lobes, ca. 15 mm. long, 1.5–2 mm. broad near the base. Flowers heterostylous (the type is a short-styled form). Corolla purple, elongate, externally strigose, especially on the lobes, bearing few, if any, stipitate glands, glabrous within, basal nectary lacking, 16–17 mm. long (20–24 mm. *fide* Aitch. & Hemsl.), tube 13 mm. long, 1.2 mm. thick at the middle, gradually widened above and becoming 3 mm. thick at the summit; throat short and broad, limb about 7 mm. in diameter, lobes ascending, apex rounded, 2 mm. long, 2.5 mm. broad. Anthers attached at the summit of the corolla tube and partly exserted into the throat, 2 mm. long. Style reaching to the middle of the corolla tube, obscurely forked at apex, 5 mm. long, lobes ca. 0.3 mm. long; stigmas 2, compressed, broader than long. Nutlets gray to brown, erect, 4–5 mm. long, obliquely attached by the broad base to a low pyramidal gynobase, with a very prominent narrow ventral keel, apex, truncate and sometimes toothed, back 2–3 mm. broad below the middle, then narrowed to the laterally compressed apex, usually with prominent longitudinal ridges paralleling the dorsal keel, surface minutely tuberculate and irregularly verrucose.

DISTRIBUTION: West Pakistan, Afghanistan (*fide* Kitamura, 1960).

West Pakistan: KURRAM AGENCY: Kurram Valley, hills behind Kaiwas, 2700–3600 m., *Aitchison 720* (K-type).

Arnebia speciosa is known from West Pakistan only from the type collection. The only other specimen collected by Kitamura is from Paghman in east Afghanistan, which is preserved in the herbarium of Kyoto University.

Arnebia speciosa is closely related to *A. benthamii* and *A. nobilis*. *Arnebia speciosa* is more like *A. benthamii* in the form of its nutlets but differs, however, in having stiffer and spreading trichomes on the stem and leaves. The calyx lobes are broader, stiffer, and the thyrse is not continuous but distinctly interrupted, with fewer shorter bracts in comparison to *A. benthamii*. *Arnebia nobilis* Rech. f. (Ann. Naturh. Mus. Wien **58**: 58. 1951), a species described from east Afghanistan [TYPE: Gazni, Djeratu, *Neubaur 836* (W)] which has its distribution in the areas of Afghanistan adjacent to the western frontier of West Pakistan, can be expected in West Pakistan. *A. speciosa* is distinguished from *A. nobilis* by having different nutlets, corolla externally strigose and hispid, and rather distinctly strigose basal leaves.

[*To be continued*]

A NEW SPECIES OF REYNOSIA (RHAMNACEAE) FROM JAMAICA

MARSHALL C. JOHNSTON

MATERIAL OF THE TREE described here was kindly sent by Mr. George R. Proctor of the Institute of Jamaica, who collected it atop a wooded limestone hill in Hanover Parish.[1] The first collection, made in August, 1965, included slightly immature fruit, which he described as "green, about 10-septate, exuding orange-yellow latex when cut." These data, taken at face value, do not point to the Rhamnaceae. The correct family was not suspected until flowers were taken from the same place in May, 1970. As it turns out, the "septa" noted are the lamellae of the ruminate endosperm of the solitary seed (FIGURE 1, d). *Reynosia*, the only genus of the family with ruminate endosperm, is represented on Cuba, Hispaniola, and Puerto Rico, and is distributed from the Virgin Islands to Florida and the Bahamas. Its apparent absence from Jamaica has been puzzling, so the present discovery is in a sense geographically fulfilling. The Jamaican plant is not a very exceptional member of the genus and can be distinguished from other species only in a suite of technical character-expressions, which nevertheless are sufficient justification for its recognition as a new species.

Reynosia jamaicensis, sp. nov.

Arbor 12-metralis; laminae ovatae vel ovales 4–7 cm. longae 2.4–5.3 cm. latae; petioli 5–10 mm. longi; pedicelli sub anthesi 2 mm. longi post anthesin 4–6 mm. longi; cupula floralis 1–3 mm. longa 1.5–2 mm. lata cellulis mucilaginis multis; sepala 4; petala 4; stamina 4; drupa (non plane matura) 15–20 mm. longa 12–15 mm. crassa.

Glabrous, unarmed tree 12 m. tall; branches and leaves opposite; two- or three-year-old branchlets with gray-brown, transversely scored and longitudinally wrinkled bark; innovations with smooth, red-tinged epidermis; blades ovate to less commonly oval, 4–7 cm. long, 2.4–5.3 cm. broad, firm in texture or even thinly coriaceous, paler beneath than above, entire-margined, with the midnerve prominent beneath and the 6 or 7 secondary nerves on each side strongly camptodrome and only slightly if at all prominent beneath; petioles very deeply grooved ventrally, 5–10 mm. long; stipules triangular, 1 mm. long, each pair joined into an eventually deciduous intrapetiolar unit. Flowers solitary or in axillary

[1] My proscrastination of several months before examining the material must now be the occasion of deep apology to George Proctor and to C. Dennis Adams. If I had examined the material promptly as requested, Dr. Adams would have been able to include the genus in his "Flowering Plants of Jamaica," a work which by this time is doubtless very near publication.

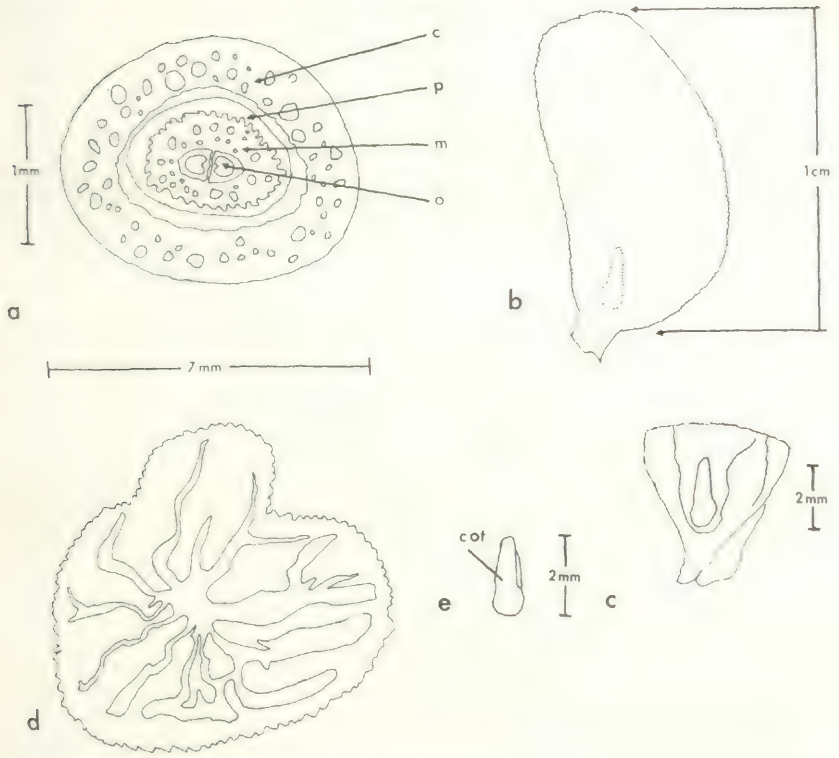


FIGURE 1. **Reynosia jamaicensis.** a, transection of the lower part of floral cup (c) with many mucilage cells and ovary showing pericarp (p), mesocarp (m), and ovule (o). b, outline of the slightly immature dried seed and persistent funiculus as seen from the side; dotted line indicating the position of the embryo within. c, longisection of the lower part of a slightly immature seed showing the embryo embedded in the corneous endosperm. d, mid-transection of slightly immature seed, showing the corneous, highly ruminate endosperm. e, embryo showing cotyledon (cot).

fascicles of 2 or 3; pedicels about 2 mm. long at anthesis, 4–6 mm. in fruit; floral cup 1–1.3 mm. long, 1.5–2 mm. broad, thick and with numerous mucilage cells (FIGURE 1, a); sepals 4, triangular, 1 mm. long, green; petals 4, obdeltoid, 0.5 mm. long, emarginate, vaguely unguiculate, cream-colored; stamens 4, about equalling the petals, the anthers brown; ovary bilocular (the partition extremely weak, FIGURE 1, a), the mesocarp with numerous mucilage cells (FIGURE 1, a); ovules solitary in each locule, erect, only one of the two maturing; raphe dorsal; style thinconic; stigma capitate, brown; fruit (not quite mature) prolate when dried, 15–20 mm. long, 12–15 mm. thick, with a thin, mucilaginous mesocarp, a thin but tough, cartilaginous or corneous endocarp, and a single large locule; funicle columnar, corneous, about 1 mm. long and thick;

seed (FIGURE 1, b, c) solitary, when fresh completely filling the cavity, in the dry condition filling less than half of it, oblong but somewhat hump-backed when dry, 9–11 mm. long, reddish brown and rugulose all over except for one smooth patch on the dorsal side near the chalazal end; endosperm ruminate (FIGURE 1, d); embryo minute (FIGURE 1, e).

Jamaica. Hanover Parish, summit of Bubby Hill, about 1 mi. southwest of Hillsbrook, about 1,450 ft. elevation, 29 August 1965, with immature fruits, *George R. Proctor 26686* (holotype, TEX; isotypes A, BM, IJ, US). Same locality, 31 May 1970, with flowers, *Proctor 31306* (A, BM, IJ, TEX, US).

Because of the presence of petals, the species falls in the subgenus NEOREYNOSIA Suessenguth (Nat. Pflanzenfam. ed. 2. 20d: 137. 1953), the systematic merits of which remain to be substantiated. Among the described species of the genus, our plant is most similar to *Reynosia krugii* Urban of Puerto Rico, which moreover matches it in the four-merous flowers and the ample size of the leaves. But in *R. krugii* the leaf blades are acuminate; stipules 2 mm. long; and the flowers only 1.5 mm. long, including both cup and calyx, are not copiously mucilaginous. Monographic work in progress may reveal other affinities.

Mucilage has not previously been reported in *Reynosia* flowers or fruits, but my dissections indicate that mucilage cells are not uncommon in the genus. However, the copious mucilage-flow in *R. jamaicensis* and its "orange-yellow" color when fresh may well be distinctive.

Mr. Proctor (in litt.) reports that Bubby Hill is a steep-sided, isolated hill which can be ascended at only one point and then only with difficulty. The foliage of *R. jamaicensis* was dark green when fresh. The density of the woodland precluded precise observations, but the crown of the tree was rather dense and irregularly shaped. Two-thirds of the associates of *R. jamaicensis* are likewise endemic Jamaican species. The other Jamaican endemics collected on Bubby Hill are: *Alvaradoa jamaicensis* Benth. (Simaroubaceae), *Bernardia* sp. nov. ined. (Euphorbiaceae), *Bursera* sp. nov. ined. (Burseraceae), *Calyptranthes acutissima* Urban (Myrtaceae), *Comocladia parvifoliola* Britton (Anacardiaceae), *Diospyros* sp. nov. ined. (Ebenaceae), *Epidendrum parvilobum* Fawcett & Rendle (Orchidaceae), *Gesneria scabra* Swartz (Gesneriaceae), *Psychotria balbisiana* DC. vel aff. (Rubiaceae), *Quiina jamaicensis* Grisebach (Quiinaceae), *Rondeletia cincta* Grisebach (Rubiaceae), *Selaginella hispida* (Willd.) A. Br. ex Urban (Selaginellaceae), *Terminalia arbuscula* Swartz (Combretaceae), *Thrinax parviflora* Swartz subsp. *parviflora* (Palmae), *Tournefortia staminea* Grisebach (Boraginaceae), *Xylopia muricata* L. (Annonaceae), *Xylosma nitida* (Hell.) A. Gray ex Grisebach (Flacourtiaceae). Also gathered were specimens of the following species which are either of wider or of unknown distribution: *Ananthacorus angustifolius* (Swartz) Underwood & Maxon (Polypodiaceae), *Anthurium cordatum* (Willd.) G. Don (Araceae), *Catopsis berteroniana* (Schultes) Mez (Bromeliaceae), *Cordia* sp. indet. (Boraginaceae), *Ficus pertusa* L.f. (Moraceae), *Guapira*

fragrans (Dum.-Cour.) Little (Nyctaginaceae). *Malpighia glabra* L. (Malpighiaceae), *Polystichum trapezoides* (Swartz) Presl (Polypodiaceae) and *Tillandsia canescens* Swartz (Bromeliaceae).

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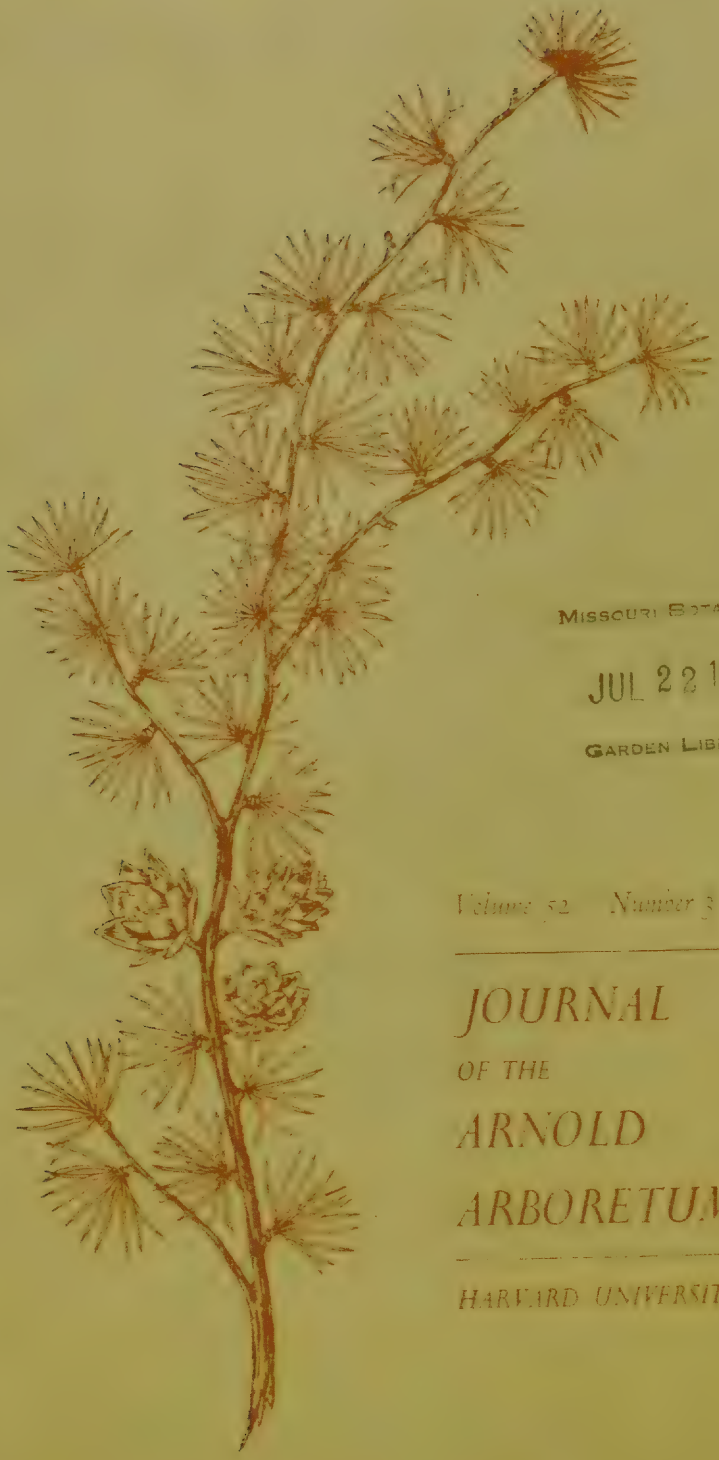
ANNOUNCEMENT

First International Congress of Systematic and Evolutionary Biology

THE SOCIETY OF SYSTEMATIC ZOOLOGY and the International Association for Plant Taxonomy have joined forces to develop this first opportunity for botanical/zoological interaction at the international level. The University of Colorado (Boulder, Colorado) has extended an invitation to meet on that campus August 4–11, 1973. The diversity of ecological situations in the surrounding countryside makes this one of the most attractive sites in North America, both aesthetically and scientifically.

To begin the planning phase, two committees have been appointed by the sponsoring organizations: the Steering Committee will be the principal organizing group; the International Committee will provide valuable advice and guidance in the development of the Congress.

Program plans at this point encompass interdisciplinary symposia and contributed paper sessions. The botanists will not convene a nomenclatural section but a zoological one on this subject is anticipated. In the next few months the outline of the program and other activities will begin to take form. All suggestions will be gratefully received, carefully considered, and as many adopted as practical or feasible. Correspondence may be addressed preferably to the Secretary, Dr. James L. Reveal, Department of Botany, University of Maryland, College Park, Maryland 20740.



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STUDIES OF PACIFIC ISLAND PLANTS, XXIII. THE GENUS DIOSPYROS (EBENACEAE) IN FIJI, SAMOA, AND TONGA[1]

ALBERT C. SMITH

IT IS AN UNDERSTATEMENT to suggest that the genus *Diospyros* L. has seemed complex to taxonomists throughout its pantropical range. In an effort to clarify the taxa occurring in Fiji, the writer has examined the available material and literature bearing on the genus in that archipelago and also in Samoa, Tonga, Niue, and the Horne and Wallis Islands. The New Hebrides would also be included in this natural phytogeographic unit, but too few specimens of *Diospyros* are available from that archipelago to make its inclusion now meaningful.

The first major work on the Ebenaceae, that of Hiern (6), provides much of the basic information on the family, but for the Malesian and Pacific regions Bakhuizen van den Brink's papers (1, 2) are a real starting point. Fosberg (3, 4) has clarified many aspects of *Diospyros* in the Pacific, and recently Green (5) has further discussed some questionable points.

Herbaria cited in the present treatment are indicated as follows: Arnold Arboretum of Harvard University (A); Bernice P. Bishop Museum (BISH); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); Department of Botany, University of Massachusetts (MASS); New York Botanical Garden (NY); Departments of Agriculture and Forestry, Suva, Fiji (SUVA); University of California, Berkeley (UC); and U.S. National Herbarium (US). Additionally a few specimens are cited that are on deposit at: British Museum (Natural History) (BM); University of California, Davis (DAV); and Muséum National d'Histoire Naturelle, Paris (P). The collaboration of administrators in making material available is greatly appreciated, as is Mr. P. S. Green's willingness to check certain matters in the English herbaria and libraries.

KEY TO SUBGENERA AND SECTIONS OCCURRING IN OUR AREA

Calyx- and corolla-lobes usually 3 (rarely 4); ovary 3- or 6-locular (rarely 4-locular), the ovules 6 (rarely 8) per ovary. . . . . Subgen. MABA.

[1] Nos. XX, XXI, and XXII of this series were published in Pacific Science, vols. 23 (1969) and 25 (1971). The present paper is based on research partially supported by a grant from the National Science Foundation.

Ovary 3-locular (rarely 4-locular), the locules 2-ovuled; ovary and fruit pilose but the latter eventually glabrate; fruiting calyx not conspicuously accrescent; stamens (in our species) 3–10 (perhaps rarely as many as 18). ..... Sect. MABA.

Ovary 6-locular, the locules 1-ovuled; ovary and fruit glabrous; fruiting calyx accrescent; stamens (in our species) 8–26. ..... Sect. RHIPIDOSTIGMA.

Calyx- and corolla-lobes usually 4 or 5 (rarely 3); ovary 8- or 10-locular, the locules 1-ovuled, 8 or 10 per ovary; ovary (in our species) sericeous but the fruit soon glabrate; fruiting calyx accrescent; stamens (in our species) 8–20 (perhaps rarely as many as 24). ..... Subgen. DIOSPYROS.

Diospyros L. subgen. **Maba** (J. R. & G. Forst.) Bakh. sect. **Maba** P. S. Green in Kew Bull. **23**: 339. 1969.

Maba J. R. & G. Forst. Char. Gen. Pl. 121. 1776; Hiern in Trans. Cambr. Philos. Soc. **12**: 106. 1873.

Ferreola Roxb. Pl. Corom. **1**: 35. 1795.

Diospyros subgen. *Maba* sect. *Forsteria* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 8. 1936, 50, *nomen illegit.* 1938.

Diospyros subgen. *Maba* sect. *Ferreola* Fosberg in Bull. Torrey Bot. Club **65**: 609. 1939; Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 429. 1941.

The type species of *Maba* is *M. elliptica* J. R. & G. Forst., and therefore, as pointed out by Green (5), MABA must be used as the epithet for the type-including section (Internat. Code Bot. Nomencl. Art. 22. 1966). This section, under one or another name, was taken by Bakhuizen definitely to include only two species, but it has been pointed out by Fosberg (3: 609) and Green (5: 340) that other taxa merit specific rank within the section. *Diospyros elliptica* (i.e. *D. ellipticifolia*) and *D. ferrea* have been discussed at length by Bakhuizen (1, 2) and the difficulties inherent in their delimitation have been considered. Each of the two species has been assigned an extended range and a perplexing array of varieties and forms. Of the characters utilized by Bakhuizen, those referring to the shape of the calyx and corolla, the stylar indument, the shape of the fruiting calyx, and the size and color of the fruit do not seem to hold in separating the complex into two meaningful taxa. What remain as usable characters refer to the type of inflorescence and the number of stamens. Characters of the inflorescence are most apparent in staminate plants, but are also visible in pistillate and fruiting material. In *D. elliptica* the inflorescence is branched, often pedunculate, and basically several- to many-flowered; in fruit this is reflected by a fructiferous axis which, if not branched, has more or less obvious scars. In *D. ferrea* the inflorescence is often subsessile and basically one- to few-flowered; in fruit this condition is indicated by a very short pulvinate-cylindric axis without perceptible scars and with a single terminal fruit. In the staminate flowers of *D. elliptica* the stamens are 3, or rarely 6; in those of *D. ferrea* the stamens are 6 to 10 or more (often 9 in our area), or perhaps very rarely reduced to 3. While such characters may not seem entirely convincing, I believe that they do serve to divide the unwieldy complex into two taxa, which one may well maintain as species in view of prevailing custom.

KEY TO SPECIES

Foliage, flowering, and fruiting parts comparatively small; leaf-blades usually 2.5–16 × 1.5–9 cm.; staminate and pistillate inflorescences with inconspicuous bracts not more than 4 × 3 mm., the calyx at anthesis 2–4 mm. long and broad, the corolla at anthesis 3–6 mm. long, the stamens about 3 mm. long; fruiting calyx 4–9 mm. in diameter; fruits 8–28 × 6–16 mm., the seeds 10–16 mm. long.

Flowering inflorescences (both staminate and pistillate) cymose, branched from base or often pedunculate, several- to many-flowered (flowers usually 3–15 or more, very rarely 2); fruiting inflorescences branched, or if simple composed of a peduncle-branchlet axis with usually obvious lateral scars, this at least 4 mm. (rarely only 2 mm.) long, with 1 to several fruits; stamens in staminate flowers 3 or occasionally 6. ..... 1. *D. elliptica.*

Flowering inflorescences usually simple, the pistillate composed of a pulvinate or cylindric peduncle 0.2–1 (–3) mm. long and 1-flowered (or flowers very rarely more than 1), the staminate similar or rarely 2- or 3-branched, the branchlets then 0.5–1 mm. long and each 1-flowered; fruiting inflorescences composed of a stout pulvinate-cylindric axis 0.5–3 mm. long without perceptible lateral scars and with a single terminal fruit; stamens in staminate flowers 6–10 or more, possibly rarely 3 (but not so noted in our area). ..... 2. *D. ferrea.*

Foliage, flowering, and fruiting parts comparatively robust; leaf-blades usually 7–21 × 3.5–11 cm.; staminate and pistillate inflorescences with a pulvinate or cylindric peduncle 1–6 mm. long, the bracts conspicuous, 6–8 mm. long, 4–6 mm. broad, the calyx at anthesis 5–9 mm. long and broad, the corolla at anthesis 14–15 mm. long, the stamens 6–9, at anthesis 6–7 mm. long; fruiting calyx 9–15 mm. in diameter; fruits solitary, at maturity 25–45 (–60) × 15–30 mm., the seeds 15–33 mm. long.

Fruits copiously pilose with short hairs and also hispidulous with stiff hairs 1–2 mm. long; fruiting inflorescences composed of a pulvinate-cylindric glomerule 1–3 mm. long; leaf-blades with 6–13 secondary nerves per side; branchlets stout, distally 2–5 mm. in diameter. ..... 3. *D. major.*

Fruits sparsely strigose with hairs 0.2–0.5 mm. long (without longer hispidulous indument); fruiting inflorescences composed of a stout cylindric peduncle 3–6 mm. long; leaf-blades with 12–22 secondary nerves per side; branchlets comparatively slender, distally 1.5–3 mm. in diameter. ..... 4. *D. christophersenii.*

1. **Diospyros elliptica** (J. R. & G. Forst.) P. S. Green in Kew Bull. 32: 340. 1969.

Maba elliptica J. R. & G. Forst. Char. Gen. Pl. 122. *t.* 61. 1776.

Tree 2–10 m. high, the young parts variously pilose, soon or eventually glabrate; petioles semiterete, rugulose, rarely exceeding 6 mm. in length (to 12 mm. in var. *savaiiensis*); leaf-blades coriaceous to chartaceous, in our varieties not exceeding 16 × 9 cm.; inflorescences cymose, branched from base or often pedunculate, usually 3–15-flowered, the bracts small and caducous, the flowers sessile; calyx cupuliform to narrowly campanu-

late or urceolate, comparatively small, at anthesis, to 4 mm. in length and diameter, the lobes 3, ovate to deltoid; corolla usually cylindric to urceolate, at anthesis 3–6 mm. long, deeply 3-lobed, often copiously sericeous without, glabrous within; staminate flowers with 3 or occasionally 6 stamens; pistillate flowers with an ovoid, sericeous or strigose ovary, the locules 2 or 3, each with 2 ovules; fruiting inflorescences usually branched, or if simple composed of a peduncle-branchlet axis with usually obvious lateral scars, this rarely less than 4 mm. long, the fruits often more than 1; fruiting calyx sessile, shallowly campanulate or rotate, not exceeding 5 mm. in length and 9 mm. in diameter, 3-lobed; fruits in our varieties not exceeding 28 × 16 mm., the seeds 1–4 maturing, black, triquetrous or semi-ellipsoid or terete.

Green's combination based on *Maba elliptica* appears to be correct to replace *D. ellipticifolia* (Stokes) Bakh. The prior binomial "*Diospyros elliptica* Hort. ex E. André" (1887) was proposed at the rank of variety and is therefore inadmissible (Internat. Code Bot. Nomencl. Art. 24. 1966). Also, *Ferreola ellipticifolia* Stokes (1812) is illegitimate (Arts. 66, 68) because *Maba elliptica* was cited in synonymy and that epithet should have been utilized. The pertinent references to the type-including taxon of *D. elliptica* are listed below under var. *elliptica*.

Although one can agree with Green in his basic circumscription of *D. elliptica*, he has, with other authors, not clearly distinguished the species from *D. ferrea*. Some of the Fijian material often referred to the latter clearly represents *D. elliptica*, which in the inclusive sense has a broad distribution from Malesia to Tonga and Samoa. In our area there appear to be seven fairly discrete varieties, all of them except var. *elliptica* requiring new trinomials.

KEY TO VARIETIES

Leaf-blades elliptic or oblong-elliptic to ovate, usually about twice as long as broad, 2.5–16 × 1.5–9 cm.; fruits not larger than 24 × 16 mm.

Petioles 1–6 mm. long; leaf-blades elliptic to oblong- or ovate-elliptic, the lowermost nerves not conspicuous nor sharply ascending, the venation not conspicuous, immersed or plane, sometimes slightly prominulous beneath; fruiting calyx with ascending or spreading lobes.

Young parts appressed-strigose or strigose-hispidulous with hairs 0.1–1 mm. long, the foliage and fruiting parts soon glabrate; leaf-blades acute to obtuse at base and often decurrent on the petiole.

Petioles 2–6 mm. long; leaf-blades 4–16 × 2–9 cm., obtuse or obtusely cuspidate or rounded at apex; fruiting calyx 5–7 mm. in diameter.

Fruiting inflorescences pedunculate with 2–several lateral branchlets, or reduced to a simple peduncle-branchlet axis, sometimes with a single maturing fruit; fruits 13–20 × 6–12 mm., the seeds 10–13 mm. long; young parts and inflorescences strigose-hirtellous with hairs 0.3–1 mm. long; leaf-blades usually 4–10 × 2–4.5 cm. . . . . 1a. var. *elliptica*.

Fruiting inflorescences congested-cymose, epedunculate, usually irregu-

larly 3–8-branched from base and with several maturing fruits; fruits 18–24 × 10–13 mm., the seeds 14–16 mm. long; young parts and (presumably) inflorescences closely appressed-strigose with hairs 0.1–0.3 mm. long; leaf-blades usually 10–16 × 5–9 cm. ..... 1b. var. *fructuosa*.

Petioles 1–2 mm. long; leaf-blades usually 3–5.5 × 1.5–2.5 cm., narrowed to an obtusely acuminate or cuspidate apex; inflorescences sericeous on external surfaces with hairs 0.2–0.3 mm. long; fruiting calyx 4–5 mm. in diameter. ..... 1c. var. *fijiensis*.

Young parts copiously tomentellous-villose or hispidulous with hairs 0.6–1 mm. long, the foliage and fruiting parts subpersistently pilose; petioles 1–2.5 (–4) mm. long; leaf-blades usually 2.5–4.7 × 1.5–2.5 cm., subcordate or rounded at base. ..... 1d. var. *foliosa*.

Petioles 5–12 mm. long; leaf-blades ovate to broadly ovate, usually 5–10 × 3–8.5 cm., abruptly narrowed at base and decurrent on the petiole, the lowermost 2 or 3 secondary nerves sharply ascending from near base, the venation conspicuous and prominulous on both sides; fruiting calyx persistently sericeous within, the lobes strongly reflexed or revolute; fruits 15–17 × 10–16 mm., strigose with hairs 0.3–1 mm. long, at length glabrate. ..... 1e. var. *savaiiensis*.

Leaf-blades lanceolate, about 4 times as long as broad, usually 8–11 ×2–3.5 cm.

Petioles 3–6 mm. long, narrowly winged nearly to base; leaf-blades chartaceous, nitid above, very early glabrate; axis of fruiting inflorescence 10–12 mm. long; fruits comparatively large, 23–28 × 13–16 mm. ..... 1f. var. *iridea*.

Petioles 2–4 mm. long, not obviously winged; leaf-blades coriaceous, dull on both sides, often persistently strigose-hispidulous on lower surface of costa; axis of fruiting inflorescence 4–6 mm. long; fruits smaller, 13–16 × 8–10 mm. ..... 1g. var. *opaca*.

1a. Diospyros elliptica var. elliptica.

Maba elliptica J. R. & G. Forst. Char. Gen. Pl. 122. *t.* 61. 1776; A. Gray in Proc. Amer. Acad. Arts **5:** 326, p.p. 1862; Hiern in Trans. Cambr. Philos. Soc. **12:** 122. 1873; Drake, Ill. Fl. Ins. Mar. Pac. 230, p.p. 1892; Hemsl. in Jour. Linn. Soc. Bot. **30:** 184. 1895; Burkill in Jour. Linn. Soc. Bot. **35:** 45. 1901; Christophersen in Bishop Mus. Bull. **128:** 172. 1935. Non "*D. elliptica* nov. var." Hort. ex E. André, 1887.

Ferreola ellipticifolia Stokes, Bot. Mat. Med. **4:** 556. *nomen illegit.* 1812.

Ebenus elliptica Kuntze, Rev. Gen. Pl. **2:** 408. 1891.

Maba buxifolia sensu Hemsl. in Jour. Linn. Soc. Bot. **30:** 184. 1895; non Pers.

Diospyros ellipticifolia Bakh. in Gard. Bull. Str. Settlem. **7:** 162. 1933, in Bull. Jard. Bot. Buitenz. III. **15:** 65, sensu typi. 1938; Yuncker in Bishop Mus. Bull. **178:** 94. 1943, in op. cit. **184:** 57. 1945.

Diospyros ellipticifolia var. *elliptica* Fosberg in Bull. Torrey Bot. Club **65:** 611. 1939; Bakh. in Bull. Jard. Bot. Buitenz. III. **15:** 431, 437. 1941; Yuncker in Bishop Mus. Bull. **220:** 212. 1959.

Diospyros major var. *elliptica* Bakh. in Bull. Jard. Bot. Buitenz. III. **15:** 431. 1941.

Diospyros ferrea sensu Yuncker in Bishop Mus. Bull. **220:** 213. 1959; non Bakh.

Tree 2.5–10 m. high, the young parts copiously strigose-hispidulous with hairs 0.3–1 mm. long, the branchlets, petioles, and leaf-blades soon glabrate; petioles 2–6 mm. long; leaf-blades subcoriaceous, elliptic to oblong-elliptic, (3–) 4–10 (–11.5) cm. long, (1.3–) 2–4.5 (–5.5) cm. broad, acute to obtuse at base, obtuse or rounded at apex, thickened and narrowly revolute at margin; inflorescences (staminate and pistillate superficially similar and distinguished only by dissection) irregularly cymose, 10–15 mm. long (including flowers), 2- or 3-times branched, usually 6–15-flowered (flowers rarely reduced to 2 or 3), some flowers often early caducous, the indument (of peduncle, branchlets, bracts, and calyx) strigose-hirtellous with hairs 0.4–0.7 mm. long, the flowers in ultimate clusters of 1–3 at tips of branchlets; calyx cupuliform, 3–4 mm. long and in diameter, copiously and closely sericeous within, the lobes ovate to deltoid, 1–2 × 2–2.5 mm.; corolla infundibular-campanulate, 5–6 mm. long, sericeous distally without, otherwise glabrous, the tube 2–2.5 mm. in diameter, the lobes oblong-ovate, 3–3.5 mm. long, 1.5–2.5 mm. broad; staminate flowers with 3 (or occasionally 6) stamens, these about 3 mm. long, glabrous, the filaments 0.6–0.8 mm. long, the anthers 2.2–2.5 mm. long, the ovary-rudiment obvious, ovoid, copiously sericeous; pistillate flowers with a sericeous ovary; fruiting inflorescences composed of a peduncle 1.5–5 mm. long and 2–several branches, with 1–several maturing fruits but with obvious scars, sometimes reduced to a peduncle and branch axis bearing 1 terminal fruit, this axis then at least 4 mm. long and with obvious lateral scars; fruiting calyx 3–5 mm. long, 5–7 mm. in diameter, glabrate; fruits ellipsoid to oblong-ellipsoid or ovoid, sometimes slightly curved, 13–20 mm. long, 6–12 mm. broad, rounded at base, obtuse at apex, glabrate; seeds 10–13 mm. long, 4–7 mm. broad.

TYPE LOCALITY: Tonga; according to Green (5) the holotype (BM) was collected by the Forsters on Tongatapu or Nomuka.

DISTRIBUTION: In discussing the typical variety (as *D. ellipticifolia* var. *elliptica*), Fosberg (3) indicated it to be widespread from Samoa to Malesia and southeastern Asia. Bakhuizen, however, in 1941(2) suggested its occurrence only in Tonga and Samoa. Specimens are now available from Tonga, Niue, Samoa, and the Wallis Islands, and a single collection from the Lau Group of Fiji shows that it also occurs there. I doubt if this natural and compact range should be further extended westward, as material from west of Lau is probably referable to other varieties as suggested by Bakhuizen (2: 429–431), although his several trinomials and quadrinomials, if accepted, will require new combinations under *D. elliptica* rather than *D. ellipticifolia*. The available specimens are from trees 2.5–10 m. high, occurring in various types of forest or thickets, or in grassland, often on limestone, at elevations from sea-level to 300 m. The trunk may attain a diameter of 25 cm.; the corolla is white to greenish yellow; and the fruit is yellow, turning orange-yellow or red.

LOCAL NAMES AND USES: The taxon is uniformly known in Tonga as *kanume*, and this name is also reported from Niue, as is *kanume uli*. In

Samoa the name is reported as *anume* or *Samoan ebony*. Yuncker reports a variety of uses in Tonga: the timber is considered good for posts, the stems are used for handicraft work, the bark is used in medicines, and the fruit is sometimes considered edible.

Fiji. VANUA MBALAVU: On limestone ridges at north end of island, *Bryan 579A* (BISH).

Wallis Islands. UVEA: Mt. Afala, *McKee 19922* (BISH, P).

Tonga. NIUAFO'OU: *Jaggar*, Oct. 1930 (BISH). NIUATOPUTAPU: Falehau, *Soakai 761* (K). VAVA'U: *Crosby 97* (K); summit of Talau, west of Neiafu, *Yuncker 16144* (BISH, GH, US); east of Neiafu, *MacDaniels 1103* (BISH); below Houma Village, *Yuncker 16131* (BISH, GH, US); near Oko'a Village, *Hotta 4925* (BISH). "VAVA'U and LIFUKA": *Harvey*, in 1855 (K). HA'APAI: Ha'ano, *Soakai 300* (K). LIFUKA: North of Pangai Village, *Yuncker 15735* (BISH, GH, US). NOMUKA: Near shore of central lake, *Yuncker 15842* (BISH, GH, US). ATATA: *Soakai 473* (K). TONGATAPU: *Graeffe 1372* (K), *1531* (K), *Lister*, Apr. 5, 1889 (K), *Setchell & Parks 15448* (K, UC); Kologa Point, *Setchell & Parks 15390* (BISH, GH, K, UC); Van Diemen's Point, *Setchell & Parks 15504* (K, UC); between Niutoua Village and the sea, *Yuncker 15124* (BISH, GH, US); 6 miles from Nuku'alofa, *MacDaniels 1083* (BISH); Hofoa, *Soakai 709* (K). 'EUA: *Lister*, Dec. 1889 (K), *Soakai 388* (K); above Houma, *Yuncker 15493* (BISH, GH, US). TONGA, WITHOUT FURTHER LOCALITY: *Graeffe* (GH, NY), *Matthews 144* (K), *Soakai 932* (K).

Niue. Near Makefu Village, *Yuncker 10104* (BISH); Vaiea Farm, *Sykes 1009* (K).

Samoa. UPOLU: Lalumanu, *Christophersen 966* (BISH, K, NY, UC, US). TUTUILA: Pago Pago, *Wilder 46* (BISH), *Diefenderfer 11* (BISH); Breakers Pt., *Wisner 123* (BISH). OFU: Top of Nuu Islet, *Garber 1102* (BISH, NY). TAU: Siulagi Point, *Garber 773* (A, BISH, K, NY, UC). SAMOA, WITHOUT FURTHER LOCALITY: *U.S. Expl. Exped.* (GH, K, NY, US), *Whitmee 249* (GH, K), *Powell 192* (K).

1b. **Diospyros elliptica** var. **fructuosa** A. C. Sm., var. nov.

Arbor ad 10 m. alta, partibus novellis pilis 0.1–0.3 mm. longis arcte strigosis, ramulis foliisque mox glabratis; petiolis crassis 2–6 mm. longis, foliorum laminis subcoriaceis, ellipticis vel elliptico-oblongis, (8–) 10–16 cm. longis, (3.5–) 5–9 cm. latis, basi obtusis, apice obtusis vel obtuse cuspidatis, margine incrassatis et anguste revolutis, costa supra subplana vel elevata subtus prominente, nervis secundariis utrinsecus 5–8 supra paullo subtus valde elevatis, rete venularum utrinque subimmerso vel plano; inflorescentiae ♀ corolla urceolata ad 4 mm. longa et 2.5 mm. diametro extus copiose sericea, lobis ovatis ad 1 mm. longis obtusis; inflorescentiis sub fructu axillaribus congesto-cymosis e basi irregulariter 3–8-ramulosis vel breviter pedunculatis, fructibus plerumque pluribus maturis exclusis 5–10 mm. diametro, ramulis et calyce pilis 0.1–0.3 mm. longis subpersistenter et arcte strigosis demum glabratis; calyce sub fructu 3–4 mm. longo 5–6 mm. diametro intus copiose sericeo, lobis late deltoideis 1.5–2 × 3–4 mm. obtusis; fructibus ellipsoideis vel obovoideis maturitate 18–24 mm. longis et 10–13 mm. latis, basi et apice obtusis vel rotundatis, seminibus 14–16 mm. longis, 5–7 mm. latis.

TYPE LOCALITY: Serua Province, Viti Levu, Fiji; the type is *Smith 9185*.

DISTRIBUTION: Known only from southern Viti Levu, Fiji, where it appears to be an infrequent component of the wet forest. Only the type collection bears detailed notes; it was taken from a tree about 10 m. high at an altitude of 30–150 m.; the mature fruit is yellow to orange or red. A few detached pistillate corollas were entangled in fruiting inflorescences. The Horne collection bears young fruits and was collected in June.

Fiji. VITI LEVU: SERUA: Hills north of Ngaloa, in drainage of Waininggere Creek, Nov. 19, 1953, *Smith 9185* (US 2192180 holotype; isotypes at BISH, K, SUVA, UC). REWA: Between Veisari River and Na Vesi, *Horne 1050a* (GH, K).

Although clearly falling within reasonable limits of *D. elliptica*, this new taxon is less closely related to other Fijian varieties than it is to var. *elliptica*, from which it is distinguished by its consistently larger leaf-blades, fruits, and seeds, the more closely appressed indument of its young parts, and its more amply branched and spreading fruiting inflorescences.

1c. **Diospyros elliptica** var. **fijiensis** (Bakh.) A. C. Sm., comb. nov.

Diospyros ellipticifolia var. *fijiensis* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 431, 437. 1941.

Diospyros ferrea var. *nandarivatensis* sensu P. S. Green in Kew Bull. 23: 342. 1969; non sensu typi.

Tree 3–10 m. high; young parts strigose with pale brown appressed hairs 0.1–0.4 mm. long, the branchlets and leaves soon glabrate, the branchlets fusco-cinereous, copiously lenticellate; petioles 1–2 mm. long; leaf-blades subcoriaceous, obscurely glandular-punctate, elliptic or ovate-elliptic, (2–) 3–5.5 (–7) cm. long, (1–) 1.5–2.5 cm. broad, acute at base and decurrent on the petiole, narrowed to an obtusely acuminate or cuspidate apex, thickened and narrowly revolute at margin, the venation immersed above, prominulous or plane beneath; staminate inflorescences short-cymose, in bud compact but to 6 mm. long and 3–10-flowered, epeduncuiate but several-branched, sericeous on external surfaces with hairs 0.2–0.3 mm. long, the bracts oblong, 0.6–1 mm. long, glabrous within; calyx in bud ovoid, to 2.5 mm. long, sericeous without, essentially glabrous within; corolla sericeous without; stamens 3, the anthers in bud about 1 mm. long; fruiting inflorescences 2- or 3-branched from base, with 1–4 maturing fruits, or composed of a pseudo-peduncle with obvious lateral scars, this 2–6 mm. long, 0.5–1 mm. in diameter, swollen at apex, persistently strigose or glabrate; fruiting calyx 2–3 mm. long, 4–5 mm. in diameter, strigose without or glabrate, the lobes broadly deltoid, subacute; fruits ellipsoid or oblong-ellipsoid, 14–20 mm. long, 7–10 mm. broad, rounded at base, obtuse at apex, at length glabrate, the seeds 11–15 mm. long.

TYPE LOCALITY: Mbua Province, Vanua Levu, Fiji; as lectotype I designate *Smith 1564*, cited below. In establishing this taxon, Bakhuizen cited

three specimens from Vanua Levu, *Smith 544*, *1564*, and *1982*, without indicating a holotype; all three are represented by duplicates in the herbarium at Bogor, where Bakhuizen presumably examined them. Since most specimens of *Diospyros* seem to be collected in fruiting rather than in flowering condition, I designate as lectotype a good fruiting specimen rather than no. *544*, which bears young staminate inflorescences.

DISTRIBUTION: Fiji, and thus far known only from Ovalau and Vanua Levu, where it has been noted as an often compact tree 3–10 m. high, growing in dense or dry forest or in ridge forest at elevations of 100–900 m. The flower-buds are pale pink, and the only flowering specimen was obtained in November; fruits were observed in April, June, and July.

LOCAL NAMES: On Vanua Levu I recorded the names *sisiruwai* (no. *1564*) and *lato* (no. *544*).

Fiji. OVALAU: Summit and adjacent slopes of Mt. Korotolutolu, west of Thawathi, *Smith 8033* (BISH, GH, K, SUVA, UC, US); slopes above Levuka, *Gillespie 4508* (BISH). VANUA LEVU: MBUA: Southern portion of Seatovo Range, in ridge forest, alt. 100–350 m., Apr. 20, 1934, *Smith 1564* (isolectotypes at BISH, GH, K, NY, UC, US). MATHUATA-THAKAUNDROVE boundary: Crest of Korotini Range, between Navitho Pass and Mt. Ndelaikoro, *Smith 544* (BISH, GH, K, NY, UC, US). THAKAUNDROVE: Uluingala, Natewa Peninsula, *Smith 1982* (BISH, GH, K, NY, UC, US).

As mentioned above, Bakhuizen originally cited three collections from Vanua Levu as representing his new variety. These same numbers had previously been cited by Fosberg (3: 610) as *D. ferrea* var. *nandarivatensis*, and Bakhuizen unfortunately repeated this (2: 441). One may assume that Bakhuizen had his 1941 manuscript already advanced when he decided to propose the new variety of *D. ellipticifolia*; although he made the proper insertions in his key (p. 431) and text (p. 437), he neglected to remove the specimen citations from p. 441. Green (5: 342), reducing Bakhuizen's variety to *D. ferrea* var. *nandarivatensis*, indicated that "examination of duplicates in the Kew Herbarium confirms that their correct disposition is under *Diospyros ferrea*." Nevertheless, as *D. elliptica* and *D. ferrea* are currently interpreted, and as maintained by Bakhuizen, these three specimens definitely belong with the former. The branching inflorescence is clearly seen in *Smith 544* (staminate) and *1564* (fruit), and furthermore no. *544* has three stamens in the staminate flower. The Fijian taxon must be referred to *D. elliptica* as a relative of var. *elliptica*, from which the distinctive leaf-shape and apex, the closer indument, and the slightly smaller fruiting calyx distinguish it as a reasonably obvious variety.

1d. **Diospyros elliptica** var. **foliosa** (Rich ex A. Gray) A. C. Sm., comb. nov.

Maba foliosa Rich ex A. Gray in Proc. Amer. Acad. Arts **5**: 326. 1862; Seem. Fl. Vit. 152. 1866; Hiern in Trans. Cambr. Philos. Soc. **12**: 113. 1873; Drake, Ill. Fl. Ins. Mar. Pac. 230. 1892.

Ebenus foliosa Kuntze, Rev. Gen. Pl. 2: 408. 1891.

Diospyros foliosa Bakh. in Bull. Jard. Bot. Buitenz. III. 15: 444, 447. 1941; A. C. Sm. in Jour. Arnold Arb. 33: 110. 1952; J. W. Parham, Pl. Fiji Isl. 160. 1964.

Tree 2–10 m. high; young parts copiously brown-tomentellous-villose or hispidulous with hairs 0.6–1 mm. long, the branchlets and leaves glabrate but sometimes tardily so, the branchlets fusco-cinereous, inconspicuously or obviously lenticellate; petioles stout, 1–2.5 (–4) mm. long; leaf-blades subcoriaceous, elliptic-oblong, (2–) 2.5–4.7 (–9) cm. long, (1.2–) 1.5–2.5 (–5.5) cm. broad, subcordate or rounded at base, obtuse or rounded at apex (rarely narrowed and short-acuminate), thickened and slightly revolute at margin, sometimes subpersistently tomentellous beneath, the venation immersed or prominulous beneath; pistillate inflorescences short-cymose, in bud compact and 3–6-flowered, copiously sericeous-tomentellous on external surfaces with golden-brown hairs 0.3–0.7 mm. long, the bracts elliptic, 1.5–2.5 mm. long, sericeous within; calyx deeply lobed, sericeous within, the lobes thick-carnose, ovate, obtuse; corolla glabrous within, the lobes sericeous without; ovary sericeous; fruiting inflorescences branched from base or short-pedunculate, with (1–) 2–5 maturing fruits, the ultimate branchlets stout, 2–4 mm. long, like the calyx subpersistently sericeous-tomentellous; fruiting calyx 2–5 mm. long, 4–7 mm. in diameter, persistently sericeous within, shallowly lobed or with obsolete lobes; fruits oblong- or ovoid-ellipsoid, 12–21 mm. long, 8–12 mm. broad, rounded at base, obtuse at apex, with subpersistent indument but eventually glabrate, the seeds 10–16 mm. long.

TYPE LOCALITY: Fiji; Gray cited the Exploring Expedition type as from "Muthuata and Ovolau" (i.e. the northern part of Vanua Levu and the island of Ovalau). It is probable that the type material came from Mathuata, from which other specimens are at hand; no collections of the taxon are definitely known from Ovalau.

DISTRIBUTION: Fiji, and known definitely only from Viti Levu and the northern part of Vanua Levu. The available specimens are noted as trees 2–10 m. high occurring in rocky forest, thin forest, or ridge forest at altitudes of 30–1100 m. The fruit is yellow, at length becoming orange or red. Pistillate flowers were obtained in December and fruits between July and November.

LOCAL NAMES: *Nganga ni sau* (*Gillespie 4062*); *ulalo* (*Smith 6439*).

Fiji. VITI LEVU: MBA: Mt. Lomalangi (Nanggaranambuluta), *Gillespie 4062* (A, BISH). NAITASIRI (?): Waimanu River basin, watershed southeast of Nasele, *Fiji Dept. Agr. 15439* (MASS, SUVA). VANUA LEVU: MATHUATA: *U.S. Expl. Exped.* (US 65907 holotype; isotype at GH); vicinity of Lambasa, *Greenwood 486* (K); Mt. Numbuiloa, east of Lambasa, *Fiji Dept. Agr. 14630* (BISH, K, SUVA); southern slopes of Mt. Numbuiloa, *Smith 6439* (A, BISH, K, US), *6443* (A, BISH, K, US). VANUA LEVU, without further data: *R. B. H. Parham 18* (A, NY).

This taxon falls within a reasonable concept of *D. elliptica*, and it can scarcely be maintained as a separate species. Its closest relationship seems to be with var. *elliptica*, from which it differs in its more copious, longer, and subpersistent indument, and in having its short-petiolate leaf-blades subcordate to rounded at base.

Bakhuizen (2: 444, 447) did not understand *Maba foliosa*, nor did he see type material. He indicated his species to be limited to New Caledonia and to include three varieties, all of which will eventually require other dispositions. Also, he placed *Diospyros foliosa* (a correct combination in spite of the misidentifications) in Sect. CUPULIFERA Fosberg, which was based (Fosberg, 3: 613) on *D. rufa* (Labill.) Fosberg; the latter binomial is to be replaced by *D. parviflora* (Schlechter) Bakh. (cf. Bakhuizen, 2: 445). Whatever the eventual circumscription of Sect. CUPULIFERA, it obviously does not extend eastward into our area. Prior to Bakhuizen's work Hiern (6: 113) had cited, in addition to the Fijian type, a New Caledonian specimen for *Maba foliosa*; this was doubtless a misidentification and it may have influenced Bakhuizen's concept of the taxon. This specimen was also probably the source of Hiern's description of the staminate inflorescence, since the original material is in fruit only; none of the specimens now at hand bears staminate inflorescences.

1e. **Diospyros elliptica** var. **savaiiensis** (Christophersen) A. C. Sm., comb. nov.

Maba savaiiensis Christophersen in Bishop Mus. Bull. **128**: 173. *fig. 26*. 1935. *Diospyros ferrea* var. *savaiiensis* Fosberg in Bull. Torrey Bot. Club **65**: 611. 1939.

Small tree 3–4 m. high, the young parts sparsely cinereous-strigose with hairs 0.2–0.4 mm. long, the branchlets and foliage soon glabrate, the branchlets slender, terete, cinereous, conspicuously lenticellate; petioles brownish to glaucous, 5–12 mm. long; leaf-blades chartaceous, ovate or broadly ovate, (4–) 5–10 cm. long, (2.5–) 3–8.5 cm. broad, abruptly narrowed at base and decurrent on the petiole, obtuse to rounded or sometimes emarginate at apex, thickened and slightly revolute at margin, the costa plane or shallowly canaliculate above, prominent beneath, the secondary nerves 5–7 per side, the lowermost 2 or 3 sharply ascending from near base, the venation conspicuous and prominulous on both sides; staminate inflorescences axillary, in very young bud composed of a copiously strigose axis 5–6 mm. long bearing 3–5 lateral sessile flowers, each subtended by an obovate bract 3–4 mm. long, this strigose without, glabrous within; calyx-bud ovoid, copiously sericeous without, with deltoid acute lobes; corolla-bud sericeous without, glabrous within; stamens minute in bud, apparently 6; fruiting inflorescences congested-cymose, sometimes borne on short defoliate branchlets suggesting racemes, composed of a stout cylindric peduncle 2–4 mm. long, this with lateral or subterminal scars and sometimes shortly branched distally or occasionally branched from base, at length glabrate, the fruits often solitary and terminal but sometimes 2 or

3 per inflorescence; fruiting calyx 2–3 mm. long, 6–9 mm. in diameter, subpersistently strigose without and copiously and persistently sericeous within with cinereous or golden hairs 0.2–0.3 mm. long, the lobes ovate, acute, about 4 × 4–5 mm., strongly reflexed or revolute; fruits ellipsoid, 15–17 mm. long, 10–16 mm. broad, rounded at base and apex, strigose with hairs 0.3–1 mm. long, at length glabrate; seeds 10–12 mm. long.

TYPE LOCALITY: Near Fangalele, Savaii, Samoa; the type is *Christophersen 3404*, cited below.

DISTRIBUTION: On the basis of presently available collections, this taxon has a remarkably limited range in the northwestern part of the island of Savaii, where it is often associated with subrecent lava flows, according to Christophersen. It has been noted as a small tree 3–4 m. high, growing in open scrub forest or low coastal forest at elevations from near sea-level to 200 m.; the fruits are orange to orange-yellow and orange-red. Young staminate inflorescences were obtained in December and fruits in November and December.

LOCAL NAME AND USE: Christophersen has noted the name as *anume* and the fruit as edible.

Samoa. SAVAII: Near Falealupo, *Christophersen 3320* (A, BISH); between Falealupo and Fangalele, *Christophersen 3328* (BISH, K, NY, UC); near Fangalele, alt. 5 m., in open scrub forest, Nov. 21, 1931, *Christophersen 3404* (BISH holotype; isotypes at A, K, NY, UC, US); Cape Puava, *Annette K. Walker*, Dec. 31, 1968 (BISH); between Aopo and Asau, *Christophersen 3428* (BISH, US).

Maba savaiiensis cannot be referred to *Diospyros ferrea*, since it has the cymose, often several-fruited inflorescences characteristic of *D. elliptica*. Rather than maintaining Christophersen's taxon as a separate species, it seems reasonable to include it in *D. elliptica*, in which it is noted as a well marked variety characterized by long petioles, broad leaf-blades with ascending lower secondaries and conspicuous venation, and a fruiting calyx persistently sericeous within and with strongly reflexed or even revolute lobes.

All the available specimens are in fruit except *Walker s.n.*, which bears very young staminate inflorescences. In this stage the inflorescences seem unusual in being basically racemose rather than cymose, but the true structure cannot yet be determined. The above description of the staminate inflorescences is based on this single specimen.

1f. **Diospyros elliptica** var. **iridea** (Fosberg) A. C. Sm., comb. nov.

Maba aff. *elliptica* Christophersen in Bishop Mus. Bull. **128:** 173. 1935.
Diospyros ellipticifolia var. *iridea* Fosberg in Bull. Torrey Bot. Club **65:** 612. 1939; Bakh. in Bull. Jard. Bot. Buitenz. III. **15:** 431, 437. 1941.
Diospyros major var. *iridea* Bakh. in Bull. Jard. Bot. Buitenz. III. **15:** 431. 1941.

Tree to 6 m. high, the young parts golden-sericeous, the branchlets soon

glabrate, very sparsely lenticellate; petioles slender, 3–6 mm. long, narrowly winged nearly to base; leaf-blades chartaceous, nitid above, lanceolate, (6–) 8–11 cm. long, (1.7–) 2–3.5 cm. broad, attenuate toward base and there revolute, obtuse at apex; pistillate inflorescences laxly cymose, 10–25 mm. long including flowers, 3–25-flowered, the peduncle (to 4 mm. long) and branchlets slender, like the calyx densely sericeous, the flowers sessile at ends of ultimate branchlets; calyx narrowly campanulate, 2–3 mm. long, the lobes deltoid, about 1 mm. long, acute; corolla cylindric, 4–5 mm. long, 1–1.5 mm. broad, sericeous on the lobes without, otherwise glabrous, the lobes ovate, about 1.5 mm. long and broad, obtuse; ovary narrowly ovoid-ellipsoid, copiously sericeous, tapering to a short style; fruiting inflorescences reduced (by loss of lateral flowers) to a combined peduncle and branch axis 10–12 mm. long, this subflexuose and marked by scars or aborted branchlets, 1–1.5 mm. in diameter, sparsely strigose, glabrate, bearing a single terminal fruit; fruiting calyx glabrate, about 5 mm. long and 7–9 mm. in diameter, the lobes broadly deltoid, obtuse; fruit ellipsoid, 23–28 mm. long, 13–16 mm. broad, rounded at base, obtuse at apex.

TYPE LOCALITY: Near Tufutafoe, Savaii, Samoa; the type is *Christophersen 3310*, cited below.

DISTRIBUTION: On the basis of the few available collections this taxon occurs sparingly on Savaii and Tutuila. It is indicated as a tree to 6 m. high, growing in forest at about 10 m. elevation; the fruits are at first yellow, becoming red when ripe. Flowers have been obtained in November and fruits in September.

Samoa. SAVAII: Near Tufutafoe, Sept. 30, 1931, *Christophersen 2772* (A, BISH, K, NY, UC, US); same locality, Nov. 22, 1931, *Christophersen 3310* (BISH holotype; isotypes at K, NY, UC, US). TUTUILA, without further data: *U.S. Expl. Exped.* (GH, US 2607582).

This well marked taxon, correctly referred to *D. elliptica* (i.e. *D. ellipticifolia*) by Fosberg, is distinct from the other varieties of our area in its lanceolate, chartaceous, shining leaf-blades, its comparatively elongate pistillate and fruiting inflorescences, and its large fruits. Although Fosberg mentions staminate flowers, a dissection indicates that the type bears pistillate inflorescences. The other originally cited collection, according to Christophersen's notes, had been obtained earlier in fruiting condition from the same tree as the type. The cited Exploring Expedition collection is indicated as from Tutuila and also bears pistillate inflorescences; it had been recognized by Gray as a variety of *Maba elliptica*, but the varietal epithet was not published.

1g. **Diospyros elliptica** var. **opaca** A. C. Sm., var. nov.

Arbor 2–3 m. alta, partibus novellis pilis 0.3–1 mm. longis copiose brunneo-strigosis, ramulis foliisque demum glabratis sed indumento costae pagina inferiore interdum persistenter strigoso-hispidulo, ramulis teretibus

fusco-cinereis saepe manifeste lenticellatis; petiolis crassis 2–4 mm. longis, laminis coriaceis utrinque opacis supra saepe impresso-glandulosopunctatis, lanceolatis, (6–) 8–11 cm. longis, 1.8–2.5 cm. latis, basim versus angustatis et in petiolum decurrentibus, apicem subacutum angustatis, margine incrassatis et valde recurvatis, costa supra plana subtus prominente, nervis secundariis utrinsecus 12–20 et rete venularum supra immersis subtus prominulis; inflorescentiis ♀ reducto-cymosis, axe cylindrico ad 4 mm. longo strigoso-hispidulo cum cicatricibus lateralibus 2 vel 3 vel e basi 2–4-ramuloso, floribus maturitate plerumque 1 vel 2; calyce urceolato ad 3 mm. longo et 2.5 mm. diametro ut pedunculo extus piloso, intus glabro, profunde 3-lobato, lobis ovatis; corolla cylindrico-urceolata maturitate ad 3 mm. longa extus copiose sericea, lobis ovatis 1.5–2 mm. longis et 1.5 mm. latis; ovario ovoideo parce strigoso in stylum brevem angustato; inflorescentiae sub fructu axe cylindrico 4–6 mm. longo cum cicatricibus lateralibus plerumque manifestis interdum e basi 2-ramuloso et calyce saepe subpersistenter strigosis demum glabratis, fructibus 1 vel 2; calyce sub fructu coriaceo campanulato vel subrotato 3–4 mm. longo 7–8 mm. diametro, lobis late ovatis circiter 2 × 4 mm. obtusis; fructu ovoideo, 13–16 mm. longo, 8–10 mm. lato, basi rotundato, apice obtuso, mox glabrato, seminibus ad 12 mm. longis.

TYPE LOCALITY: Serua Province, Viti Levu, Fiji; the type is *Fiji Dept. Agr. 14883*.

DISTRIBUTION: Known only from the type collection, indicated as a small tree 2–3 m. high growing in forest; the fruit is green, becoming yellow to dark red.

Fiji. VITI LEVU: SERUA: Bank of upper Navua River, Apr. 22, 1966, *Fiji Dept. Agr.* (coll. *D. Koroiveibau & I. Qoro*) *14883* (BISH holotype; isotypes at MASS, SUVA).

Although known from a single collection, this taxon seems definitely to fall into *D. elliptica*, but it is not close to other Fijian varieties. It is more suggestive of the Samoan var. *iridea*, with which it closely agrees in leaf-shape. However, var. *opaca* is well characterized by its short, unwinged petioles, its comparatively thick and dull leaf-blades with subpersistent indument, its shorter fruiting inflorescences, and its substantially smaller fruits.

2. **Diospyros ferrea** (Willd.) Bakh. in Gard. Bull. Straits Settlem. 7: 162. 1933, in Bull. Jard. Bot. Buitenz. III. **15**: 50. 1938, in op. cit. III. **15**: 431, p. p. 1941.

Ehretia ferrea Willd. Phytographia 4. *t. 2, fig. 2.* 1794.

Tree 2–15 m. high, the young parts strigose, the branchlets and foliage soon glabrate; petioles in our varieties not exceeding 5 mm. in length; leaf-blades coriaceous to chartaceous, in our varieties not exceeding 21 × 8 cm. and rarely more than 12 × 5.5 cm.; pistillate inflorescences composed of

a pulvinate or cylindric peduncle usually no more than 1 mm. long and usually bearing a single sessile flower subtended by 2 bracts; staminate inflorescences similar or reduced-cymose, rarely 2- or 3-branched, the branchlets then not more than 1 mm. long and each 1-flowered; calyx cupuliform to campanulate, comparatively small, at anthesis to 3.5 mm. in length and 4 mm. in diameter, the lobes 3, ovate to deltoid; corolla usually urceolate to campanulate-infundibular, at anthesis 4.5–5.5 mm. long, 3- or occasionally 4-lobed, sericeous without, glabrous within; staminate flowers with 6–10 stamens, these sometimes more or rarely 3 (but not so noted in our area); pistillate flowers with an ovoid to globose, strigose or sericeous ovary, the locules usually 3 (sometimes 2 or 4), each with 2 ovules; fruiting inflorescences simple, composed of a stout pulvinate-cylindric axis 0.5–3 mm. long, this without perceptible lateral scars and with a solitary terminal fruit; fruiting calyx sessile, broadly campanulate or rotate, not exceeding 4 mm. in length and 8 mm. in diameter, 3-lobed; fruits in our varieties not exceeding 20 × 15 mm., the seeds 1–3 (or to 6) maturing, black, triquetrous or semi-ellipsoid or oblong-ellipsoid.

In the inclusive sense and under various trinomials *D. ferrea* has been accredited with a wide distribution, extending at least from Malesia into Polynesia and Hawaii. However, as here circumscribed the species does not occur in Tonga or Samoa; material from those archipelagos so identified is better referred to *D. elliptica*.

With the removal of certain western Polynesian taxa that have sometimes been referred to an extended concept of *D. ferrea* (i. e. the taxa in this paper discussed as *D. elliptica* var. *savaiiensis*, *D. major*, and *D. christophersenii*), it appears that true *D. ferrea* occurs within our area only in Fiji. Even here it is less complex and diverse than the related *D. elliptica*, being represented by three varieties as noted below. Nomenclatural complications have been caused by misidentifications and by disagreement as to the limits of taxa. An extended consideration of the trinomial *Diospyros ferrea* var. *glabrescens* (Seem.) P. S. Green is required.

Green's trinomial is based on *Maba elliptica* var. *glabrescens* Seem., which appears to me to be a provisional name under the definition of Art. 34 (Internat. Code Bot. Nomencl. 1966). Seemann's entire entry is herewith quoted:

> "My nos. 295, 296, and 297, and Storck's n. 898, might be distinguished as a variety *glabrescens* of *M. elliptica*, as the nascent branches very quickly become glabrous."

Use of the word "might" seems to indicate that Seemann did not accept this trinomial, but merely proposed it in anticipation of the future acceptance of the group concerned. In his prior discussion of *M. elliptica* as a species he had listed the same four numbers, pointing out that *M. elliptica* had also been collected in the Tongan Islands, Isle of Pines, and New Caledonia.

In such marginal cases, when it is not entirely clear whether an author was actually "accepting" a name in the nomenclatural sense, it seems ad-

visable to consider his method of working and publishing. For his period Seemann was a meticulous botanist, and he leaves no doubt in the reader's mind when he wishes to "accept" a taxon. Seemann seems not to have made much use of the rank of "variety" in *Flora Vitiensis*, but nevertheless one finds some 30 or 40 instances in which varietal combinations are accepted; these trinomials are invariably followed by Latin descriptions or diagnoses and by the unequivocal citation of specimens. Most such varieties are those of prior authors but for an example of Seemann's treatment of one of his own new varieties, the reader is referred to *Hibiscus tiliaceus* var. *purpurascens* (page 18). In view of the uniformly meticulous presentation of "accepted" varieties in *Flora Vitiensis*, one may regard the casual note on *Maba elliptica* var. *glabrescens* as provisional and not as a nomenclaturally acceptable proposal of a trinomial. In this interpretation Green's trinomial and also his quadrinomials (f. *glabrescens* and f. *impressa*) are to be rejected as illegitimate under the provisions of Art. 63.

Among the specimens cited by Seemann in the above quotation, *Storck 898* has been indicated by Green as the lectotype and may therefore be taken as the source of the name *Maba elliptica* var. *glabrescens*, regardless of the provisional status of that name. This specimen falls into var. *phlebodes* of the present treatment. The other three numbers cited by Seemann, although "paratypes," have no bearing on the disposition of the name. Two of these numbers, *Seemann 296* and *297*, also fall into var. *phlebodes*; the third, *Seemann 295*, falls into var. *gillespiei*. It must be noted that Green equated *Storck 898* with *D. ferrea* var. *subimpressa* Fosberg, typified by *Gillespie 2324*. However, Green did not examine the latter collection but based his concept of var. *subimpressa* on *Degener & Ordonez 13634* and *14196*. These latter collections indeed agree with *Storck 898* and are here referred to var. *phlebodes*. My proposed reduction of var. *subimpressa* to var. *gillespiei* is discussed under the latter.

KEY TO VARIETIES

Peduncle (or peduncle-branchlet axis) of fruiting inflorescences 0.5–3 mm. long, the fruiting calyx soon glabrate on both surfaces, the lobes not reflexed, the fruit closely strigose and very early glabrate; petioles 1–5 mm. long; leaf-blades with inconspicuous and often immersed venation, the lowermost secondary nerves not conspicuously ascending.

Petioles 1–3 mm. long; leaf-blades coriaceous, elliptic to oblong-elliptic, about twice as long as broad, obtuse at base, obtuse to rounded at apex. . . . . 2a. var. *gillespiei*.

Petioles 2–5 mm. long, conspicuously winged distally; leaf-blades thin-coriaceous or chartaceous, lanceolate or oblong-lanceolate, about three times as long as broad, narrowed to a subacute base and long-decurrent on the petiole and there conspicuously revolute, narrowed to an obtusely acuminate or cuspidate apex. . . . . 2b. var. *nandarivatensis*.

Peduncle of fruiting inflorescences pulvinate-cylindric, less than 1 mm. long, the fruiting calyx copiously strigose without and persistently densely sericeous within, the lobes spreading or reflexed, the fruit copiously and subpersistently sericeous with hairs 0.3–1 mm. long; petioles inconspicuous, essen-

tially none or to 2 mm. long; leaf-blades with conspicuous and often prominulous venation, the lowermost 2 or 3 secondary nerves sharply ascending from near base of blade or from petiole. . . . . 2c. var. *phlebodes*.

2a. **Diospyros ferrea** var. **gillespiei** Fosberg in Bull. Torrey Bot. Club **65**: 610. 1939; Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 435, 441. 1941; J. W. Parham, Pl. Fiji Isl. 160. 1964.

Diospyros ferrea var. *subimpressa* Fosberg in Bull. Torrey Bot. Club **65**: 611. 1939; J. W. Parham, Pl. Fiji Isl. 160. 1964.

Diospyros ferrea var. *gillespiei* f. *impressa* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 435, *nomen illegit*. 1941.

Diospyros ferrea var. *gillespiei* f. *subimpressa* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 435. 1941.

Diospyros ferrea var. *glabrescens* f. *impressa* Bakh. ex P. S. Green in Kew Bull. **23**: 341, *nomen illegit*. 1969.

Tree 2–15 m. high, the young parts inconspicuously brown-strigose with hairs 0.2–0.4 mm. long, the branchlets slender, cinereous, conspicuously lenticellate; petioles semiterete or shallowly canaliculate, 1–3 mm. long; leaf-blades coriaceous, elliptic to oblong-elliptic, (3–) 3.5–12 (–21) cm. long, (1.2–) 1.5–5 (–8) cm. broad, obtuse at base and decurrent on the petiole, obtuse or obtusely cuspidate to rounded or faintly emarginate at apex, thickened and slightly revolute at margin, the costa depressed or impressed above, prominent beneath, the other venation immersed or the secondaries slightly impressed above; pistillate inflorescences axillary, simple (rarely minutely branched and with second or third soon caducous flowers), the peduncle 0.5–1 (–3) mm. long and 0.5–1 mm. in diameter, glabrate, the bracts ovate-oblong, about 1.5 mm. long, obtuse; calyx at anthesis 3–3.5 mm. long, sparsely strigose without, closely sericeous within; corolla urceolate, at anthesis 5–5.5 mm. long, the lobes ovate-oblong, obtuse, 2.5–3 mm. long; ovary ovoid, closely strigose; fruiting inflorescences composed of a peduncle 0.5–2 (–3) mm. long and 1.5–2 mm. in diameter, glabrate, slightly swollen at apex; fruiting calyx 3–4 mm. long, 5–8 mm. in diameter, soon glabrate on both surfaces, the lobes broadly ovate, rounded or obtuse; fruit ellipsoid to oblong-ellipsoid, sometimes slightly curved, 13–20 mm. long, 8–15 mm. broad, rounded at base and apex, soon glabrate; seeds 12–15 mm. long.

Type locality: Naitasiri Province, Viti Levu, Fiji; the type is *Gillespie 2146*, cited below. The type of *D. ferrea* var. *subimpressa*, here reduced to synonymy, is *Gillespie 2324*, also cited below, from Rewa Province, Viti Levu.

Distribution: The variety is endemic to Fiji and is thus far known from the islands of Viti Levu, Kandavu, Ovalau, and Vanua Levu, where it has been recorded as an often slender tree 2–15 m. high; it occurs in open or dense forest or in woods at altitudes of 15–960 m. Flowering specimens seem infrequently collected and have been noted only in November, but fruiting material has been obtained between April and November; the fruits are yellow to orange or red.

LOCAL NAMES: Recorded only once each are the names *mathendre* (*Smith 7169*) and *mamba* (*Fiji Dept. Agr. 791*); the latter is more or less generic in Fiji.

Fiji. VITI LEVU: MBA: Mountains nears Lautoka, *Greenwood 200* (K). SERUA: Near summit of Mt. Tikituru, *Fiji Dept. Agr. 14481* (BISH, SUVA). NAMOSI: Hills north of Wainavindrau Creek, *Smith 8443* (BISH, GH, K, SUVA, UC, US); summit of Mt. Nambui, *Fiji Dept. Agr. 14549* (BISH, SUVA); Nakavu, on Navua River, *Horne 823* (K). NAITASIRI: Nanggarathangithangi, Mendrausuthu Range, *Fiji Dept. Agr. 15031* (BISH, SUVA); Waindrandra Creek, *Fiji Dept. Agr. 791* (A, SUVA); vicinity of Tamavua, *Gillespie 2450* (BISH, NY); beyond Tamavua Village, alt. 150 m., Aug. 9, 1927, *Gillespie 2146* (BISH holotype; isotypes at A, US). TAILEVU: Hills east of Wainimbuka River, vicinity of Ndakuivuna, *Smith 7169* (BISH, GH, K, US). REWA: Nggoya Forest Reserve, *Fiji Dept. For. 475* (SUVA); Mt. Korombamba, Aug. 23, 1927, *Gillespie 2324* (BISH holotype of *D. ferrea* var. *subimpressa*); same locality, *Webster & Hildreth 14045* (DAV, MASS), *Fiji Dept. Agr. 17368* (A, MASS, NY, SUVA). KANDAVU: Hills above Namalata and Ngaloa Bays, *Smith 126* (BISH, GH, K, NY, UC, US). OVALAU: Hills west of Lovoni Valley, on ridge south of Mt. Korolevu, *Smith 7644* (BISH, GH, K, SUVA, UC, US); Mt. Ndelaiovalau, east of Lovoni Valley, *Fiji Dept. Agr. 14501* (BISH, SUVA). VANUA LEVU: MATHUATA: Southern slopes of Mt. Numbuiloa, east of Lambasa, *Smith 6367* (A, BISH, K, US). FIJI, without further locality, *Seemann 295* (GH, K).

I have found no possible way to maintain Fosberg's two varietal taxa even as forms; the type specimens are scarcely distinguishable. Of var. *subimpressa* Fosberg notes: "Very close to var. *gillespiei*, differing chiefly in the shape of the fruit and in the less conspicuously impressed veins." In fact, however, some of the fruits on the two types are practically indistinguishable. The secondary nerves in var. *gillespiei* are more sharply impressed above, and in general the leaf-blades are more coriaceous and with more immersed reticulation, but these characters lose significance when other representatives of the Fijian population are examined.

In first combining the two varieties and reducing them to forms, Bakhuizen (2: 435) used the varietal epithet *gillespiei* and must therefore be followed. His type form of this variety was newly named "f. *impressa*," an inadmissible procedure.

2b. **Diospyros ferrea** var. **nandarivatensis** (Gillespie) Fosberg in Bull. Torrey Bot. Club **65**: 610. 1939, in op. cit. **67**: 417. 1940; Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 435, 441. 1941; J. W. Parham, Pl. Fiji Isl. 160. *fig. 61, B* (err. legend as *A*). 1964.

Maba nandarivatensis Gillespie in Bishop Mus. Bull. **74**: 13. *fig. 15*. 1930.

Slender tree 3–8 m. high, the young parts inconspicuously strigose with hairs 0.2–0.5 mm. long, the branchlets slender, fusco-cinereous, inconspicuously or obviously lenticellate; petioles slender, semiterete, narrowly winged distally, 2–5 mm. long; leaf-blades thin-coriaceous or chartaceous, lanceolate or oblong-lanceolate, (3–) 4–9 cm. long, (1–) 1.5–3 cm. broad,

narrowed to a subacute base and long-decurrent on the petiole and there conspicuously revolute, narrowed to an obtusely acuminate or cuspidate apex, slightly thickened and often undulate at margin, the costa impressed above, prominent beneath, the secondaries numerous, spreading, with the veinlets subimmersed or prominulous beneath; staminate inflorescences reduced-cymose, the peduncle simple, slender, about 0.5 mm. long, sparsely strigose, with 2 or 3 minute branchlets at apex, these 0.5–1 mm. long, the bracts oblong, 0.8–1.5 mm. long, glabrate; flowers usually 2 or 3; calyx in bud ovoid, about 3 mm. long, obscurely strigillose without; corolla urceolate in bud, copiously sericeous without; stamens 9 or 10, glabrous, the ovary-rudiment minute, hispidulous; pistillate inflorescences simple, the peduncle about 0.5 mm. long, or perhaps sometimes branched like the staminate inflorescences, the calyx and corolla in bud as in the staminate flower; fruiting inflorescences simple, the peduncle-branchlet axis 0.5–3 mm. long and swollen at apex, soon glabrate; fruiting calyx 2–4 mm. long, 4–8 mm. in diameter, soon glabrate on both surfaces, the lobes broadly ovate-deltoid; fruit ellipsoid or obovoid to oblong-ellipsoid, 11–20 mm. long, 7–11 mm. broad, rounded at base and apex, soon glabrate; seeds 12–13 mm. long.

TYPE LOCALITY: Nandarivatu, Mba Province, Viti Levu, Fiji; the type is *Gillespie 3848*, cited below.

DISTRIBUTION: Endemic to Fiji, and thus far known only from upland Viti Levu at altitudes of 725–1050 m. It is noted as an often slender tree 4–8 m. high, occurring in dense forest; the fruits are yellow to red. Seasons do not appear marked, as flowers have been obtained in July and November and fruits in various months.

LOCAL NAMES: Recorded only once each are the names *vaundrai ni singa* (*Gillespie 3848*), *mbama* (*Degener 14434*), and *mbamathendru* (*Smith 5564*).

Fiji. VITI LEVU: MBA: Slopes and summit of Mt. Ndelaiyoö, on escarpment west of Nandarivatu, *Smith 5074* (A, BISH, K, US); Nandarivatu, Nov. 17, 1927, *Gillespie 3848* (BISH holotype; isotype at UC); vicinity of Nandarivatu, *Parks 20602* (BISH, UC, US), *Gillespie 3764* (BISH, NY, UC); Mt. Lomalangi (Nanggaranambuluta), *Fiji Dept. Agr. 14447* (BISH, SUVA); Mt. Matomba, Nandala, *Degener 14434* (A, K, NY, US). NANDRONGA & NAVOSA: Northern portion of Rairaimatuku Plateau, between Nandrau and Nanga, *Smith 5564* (A, BISH, K, US).

These first two Fijian varieties of *D. ferrea* are only questionably separable; no differences in inflorescences or fruits are of consequence, and the foliage differences pointed out in my key are far from strong. In general, however, the few specimens listed as var. *nandarivatensis* are distinguishable in their thinner, narrower leaf-blades, which are conspicuously revolute proximally and long-decurrent on the petiole, and more gradually narrowed apically. However, some of these distinctions are weakened by the two Ovalau collections cited under var. *gillespiei*.

It is interesting to look into the past interpretations of the present taxon. In proposing it as a species, *Maba nandarivatensis*, Gillespie cited his no. *3848* (type) and *3764* and *Parks 20602*; all come from Nandarivatu and clearly belong together. In 1939 Fosberg cited the type, three Vanua Levu collections of Smith (*544*, *1564*, *1982*) which actually represent *D. elliptica* var. *fijiensis*, and a Kandavu specimen (*Smith 126*) which I refer to *D. ferrea* var. *gillespiei*. In view of this mixture, it is not surprising that Fosberg remarked that this taxon seemed to connect *D. ferrea* and *D. ellipticifolia*. The Micronesian specimens cited as *D. ferrea* var. *nandarivatensis* by Fosberg in 1939 and also later (4: 417) appear to have no close relationships to any of the Fijian varieties. Green (5: 342), in maintaining *D. ferrea* var. *nandarivatensis*, cited only the three Smith collections from Vanua Levu mentioned above, and consequently he was not impressed by the close similarity of Gillespie's taxon to the other two Fijian varieties proposed by Fosberg.

It is quite clear that much of the Fijian material of *D. ferrea* (once the components really belonging to *D. elliptica* are removed) is so closely similar that vars. *gillespiei* and *nandarivatensis* are with difficulty maintainable. However, a third variety, the following, appears to be much stronger.

2c. **Diospyros ferrea** var. **phlebodes** A. C. Sm., var. nov.

Maba elliptica sensu Seem. Fl. Vit. 152, p. p. 1866; non J. R. & G. Forst.
Maba elliptica var. *glabrescens* Seem. Fl. Vit. 152, *nomen provis.* 1866; Hiern in Trans. Cambr. Philos. Soc. **12**: 118, *nomen.* 1873.
Maba buxifolia sensu A. C. Sm. in Bishop Mus. Bull. **141**: 121, p. p. 1936; non Pers.
Diospyros ferrea var. *glabrescens* P. S. Green in Kew Bull. **23**: 341, *nomen illegit.* 1969.
Diospyros ferrea var. *glabrescens* f. *glabrescens* P. S. Green in Kew Bull. **23**: 341, *nomen illegit.* 1969.

Arbor 4–8 m. alta, partibus novellis pilis pallidis vel fuscis 0.2–0.5 mm. longis strigosis, ramulis gracilibus saepe conspicue lenticellatis; petiolis complanatis crassis rugulosis subnullis vel ad 2 mm. longis, laminis subcoriaceis, ovatis vel oblongo-ellipticis vel oblongo-lanceolatis, (3–) 4–10 cm. longis, (1.5–) 2–5.5 cm. latis, basi rotundatis vel obtusis abrupte angustatis et in petiolum decurrentibus, apice obtusis vel obtuse cuspidatis margine incrassatis saepe pallidis, costa supra plana vel canaliculata subtus elevata, nervis secundariis utrinsecus 4–9, inferioribus 2 vel 3 basim versus vel e petiolo valde adscendentibus cum rete venularum utrinsecus conspicuis et subplanis vel prominulis; inflorescentiae ♀ pedunculo 0.2–0.8 mm. longo ad 1 mm. diametro apice incrassato, bracteis oblongo-ovatis 1.2–1.8 mm. longis ad 3 mm. latis apice rotundatis mox glabratis et caducis; calyce cupuliformi ad 3 mm. longo et 4 mm. diametro utrinque pilis ad 0.2 mm. longis copiose sericeo, lobis late ovatis circiter 1 × 3 mm. apice obtusis; corolla campanulato-infundibulari 4.5–5 mm. longa ad 3

mm. diametro extus superne copiose sericea intus glabra, lobis 3 vel 4 ovatis subacutis circiter 2.5 × 2 mm.; ovario ovoideo-globoso pilis pallidis 0.3–0.5 mm. longis copiose sericeo; inflorescentiae sub fructu pedunculo minus quam 1 mm. longo; calyce sub fructu 2–3 mm. longo 5–8 mm. diametro extus copiose strigoso intus pilis 0.3–0.5 mm. longis persistenter dense sericeo, lobis patentibus vel reflexis late ovatis ad 2 × 4–5 mm. apice rotundatis; fructu subgloboso vel oblongo-ellipsoideo 8–13 mm. longo 6–13 mm. lato, basi rotundato, apice obtuso, pilis 0.3–1 mm. longis copiose et subpersistenter sericeo, seminibus 8–9 mm. longis.

TYPE LOCALITY: Nggalito Island, Malolo Group, Mamanuthas, Fiji: the type, *O. & I. Degener 32224*, cited below, is a specimen with good pistillate inflorescences as well as fruits.

DISTRIBUTION: The new variety, endemic to Fiji, is widely distributed within the group, often found in coastal areas or on smaller islands, where it occurs at altitudes from sea-level to 300 m. It has been noted as a sometimes spreading tree 4–8 m. high, in beach thickets, dry or dense forest, or on open hillsides; the fruit is yellow to pinkish yellow or red. No periodic flowering or fruiting season is apparent.

LOCAL NAMES: *Kaukauloa* (*Fiji Dept. Agr. 13725*) or *kauloa* (*Tothill F436*); both these names are more or less generic in Fiji.

Fiji. MAMANUTHAS (west of Viti Levu): MALOLO GROUP: Nggalito Island, in forest near coast, near sea-level, Feb. 7, 1969, *O. & I. Degener 32224* (BISH holotype). VITI LEVU: MBA: North of Lomolomo, *Degener & Ordonez 13634* (A, BISH, K, NY, UC, US). RA: Near Penang, *Greenwood 761* (K); vicinity of Rewasa, near Vaileka, *Degener 15496* (A, NY, US). MBENGGA: Ndakuimbengga, *Fiji Dept. Agr. 13721* (BISH, K, SUVA); Lalati, *Fiji Dept. Agr. 13725* (BISH, K, SUVA); Uthuinanggaratu, *Fiji Dept. Agr. 2087* (A, SUVA). OVALAU: Waililevu, *Fiji Dept. Agr. 17020* (BISH, K, SUVA). KORO: *Tothill 577b* (K). VANUA LEVU: MATHUATA: *Seemann 297* (GH, K); Ndreketi River, *Fiji Dept. For. 251* (BISH, MASS, SUVA); Nanduri, *Tothill F436* (K); vicinity of Lambasa, *Greenwood 565* (K). THAKAUNDROVE: Maravu, near Salt Lake, *Degener & Ordonez 14196* (A, BISH, K, NY, UC, US). TAVEUNI: Vicinity of Somosomo, *Seemann 296* (GH, K). MATUKU: On rocky shore, *Tothill 577a* (K); on summit ridge, *Bryan 267* (BISH). KANATHEA: *Graeffe 1364* (K). FIJI, without further locality: *U.S. Expl. Exped.* (US 653978), *Storck 898* (source of the name *Maba elliptica* var. *glabrescens*, GH, K), *Horne 390* (GH, K).

Of the components of *D. ferrea* in Fiji, the variety here described is the most distinct, differing from the only other two varieties that can be maintained, vars. *gillespiei* and *nandarivatensis*, in distinctive foliage and fruit characters as noted in my key. The new variety is curiously suggestive of the Samoan *D. elliptica* var. *savaiiensis*, although in inflorescence characters the latter cannot be placed with *D. ferrea*. Like *D. elliptica* var. *savaiiensis*, the new variety has its fruiting calyx persistently pilose and with reflexed lobes, its fruits also subpersistently pilose with unusually long hairs, and the lowermost secondary nerves of its leaf-blades

similarly sharply ascending. The two taxa differ not only in their inflorescence-type and in their fruiting peduncles, but obviously in the length of their petioles. Nevertheless, the occurrence of such similar general aspects in adjacent archipelagos indicates a complex and reticulate relationship among taxa of the *D. elliptica* — *D. ferrea* group.

Reasons for describing the present taxon as new, rather than accepting for it the varietal epithet *glabrescens*, were discussed above in my introductory comments on *D. ferrea*.

3. **Diospyros major** (Forst. f.) Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 429. 1941.

Maba major Forst. f. Pl. Esculent. Ins. Oc. Austr. 54, "*maior*." 1786, Fl. Ins. Austr. Prodr. 92, "*maior*." 1786; A. DC. in DC. Prodr. **8**: 242. 1844; Hiern in Trans. Cambr. Philos. Soc. **12**: 125. 1873.

Maba andersonii Seem. Fl. Vit. 152, *nomen*. 1866.

Maba andersoni Soland. ex Hiern in Trans. Cambr. Philos. Soc. **12**: 124. 1873.

Maba lateriflora Hiern ex Baker in Jour. Linn. Soc. Bot. **20**: 366. 1883; Burkill in op. cit. **35**: 45. 1901.

Ebenus andersoni Kuntze, Rev. Gen. Pl. **2**: 408. 1891.

Diospyros lateriflora Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 8. 1936; Fosberg in Bull. Torrey Bot. Club **65**: 612. 1939, in op. cit. **67**: 417. 1940; Yuncker in Bishop Mus. Bull. **220**: 213. 1959; J. W. Parham, Pl. Fiji Isl. 160. 1964.

Maba globosa sensu A. C. Sm. in Bishop Mus. Bull. **141**: 121. p. p. *fig. 63*, non sensu typi. 1936.

Diospyros ellipticifolia var. *major* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 431. 1941.

Diospyros major var. *andersoni* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 431. 1941.

Diospyros ferrea var. *lateriflora* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 435, 442. 1941.

Diospyros andersonii P. S. Green in Kew Bull. **23**: 339. 1969.

Tree 3–15 m. high, or occasionally a shrub, the branchlets subterete, stout, distally 2–5 mm. in diameter, with projecting lenticels, glabrous except on strigose innovations; petioles 2–15 mm. long, stout, 1.5–3 mm. in diameter, subterete or shallowly canaliculate; leaf-blades coriaceous or subcoriaceous, oblong or elliptic to ovate-oblong, (4–) 7–21 cm. long, (2.5–) 4–11 cm. broad, narrowly subcordate or rounded to cuneate at base, obtuse or rounded at apex, the costa usually plane above and prominent beneath, the secondary nerves 6–13 per side, plane or slightly raised on both surfaces, the veinlet-reticulation often immersed, usually slightly raised on both surfaces; staminate inflorescences axillary or borne along branchlets, glomerulate, the peduncle woody, irregularly subglobose or short-cylindric, 1–3 mm. long, hispidulous-sericeous distally; flowers sessile, often congested, 3–5, bracteate, the bracts conspicuous, obovate, 6–8 mm. long, 4–6 mm. broad, obtuse at apex, copiously sericeous without, glabrous within, caducous; calyx cupuliform, 5–9 mm. long and in

apical diameter, copiously sericeous on both sides (except on tube within) with hairs 0.5–0.8 mm. long, the lobes 3, deltoid-ovate, 2–5 mm. long and broad, subacute; corolla cylindric-campanulate, at anthesis 14–15 mm. long and about 5 mm. in diameter at middle, copiously sericeous like the calyx without, glabrous within, the lobes 3, ovate-oblong, 5–6 × 3–4 mm., subacute; stamens 6–9, free or sometimes coherent at base, 6–7 mm. long, the filaments slender, glabrous, about 3 mm. long, the anthers 3–4 mm. long, the ovary rudimentary, with associated marginal hairs; pistillate inflorescences similar but with a solitary apical flower, the flowers similar to the staminate, the ovary sericeous, 3-locular, the locules 2-ovulate; fruiting inflorescences composed of a pulvinate-cylindric glomerule 1–3 mm. long and 2–3.5 mm. broad, often hispidulous and slightly swollen distally, sometimes borne on defoliate branchlets; fruiting calyx sessile, not conspicuously accrescent, coriaceous, 9–15 mm. in diameter, copiously strigose-hispidulous without and sericeous within, the lobes broadly ovate, 3–5 × 5–8 mm., rounded at apex; fruit solitary, ellipsoid or ovoid, at maturity 25–45 (–60) mm. long and 15–30 mm. broad, obtuse at base, apically subacute to base of the stylar remnant, closely pilose with copious short hairs and also hispidulous with stiff hairs 1–2 mm. long, eventually but tardily subglabrescent, the seeds oblong, triquetrous, 15–25 mm. long.

Type locality: Tonga. Mr. P. S. Green has kindly sought for an extant Forster type in the British Museum collections, but none has been disclosed. This is not surprising, since the description was based entirely on a fruit, or perhaps was even a second-hand description taken from Cook (Voyage to the Pacific Ocean, 393. 1784): ". . . a smaller tree, that bears a rounded oval nut, two inches long, with two or three triangular kernels, tough and insipid, called *mabba*, most frequently planted near their houses." Forster's original reference is here quoted in full:

> "Huius fructus cum illo Mabae ellipticae nostrae in omnibus convenit, praeterquam quod triplo maior sit, bipollicaris scilicet, in loculamentis fovens nucleos triquetros, tenaces et insipidos, tamen inter edulia ab incolis usurpatos. Incolae insularum Tongatabu, Namoka, E-uwa, Hapa-i, et ceterarum quae ad archipelagum amicorum pertinent, hanc arborem teste Cookio in noviss. itin. tom. I. p. 393. circa tuguria plantare solent. Nobis non nisi drupa, ab incolis iisdem venum asportata innotuit, cui nomen *Maba* imposuerunt."

In the absence of an extant type specimen, his description may be taken as the type (Internat. Code Bot. Nomencl. Art. 9, Note 1. 1966).

Two other epithets are involved in the synonymy of *D. major*. The type specimen of *Maba andersoni*, discussed by Green (5: 339), was collected by or for *Capt. Cook* (BM) on his third voyage, in Tonga.

In the original description of *Maba lateriflora*, Baker (on behalf of Hiern) cited three Horne collections from Fiji: *201* (Ovalau), *s.n.* (Rambi), and *1013* (Viti Levu). The Kew sheet of the last of these is an excellent fruiting specimen, which bears a handwritten note from Hiern to Baker; I designate this as the lectotype, although perhaps unnecessarily

since the name falls into synonymy, as discussed by Green (5: 330). Horne's field label for no. *1013* indicates "common in the province of Navosa," implying the Singatoka drainage; it was very probably obtained within the present Province of Nandronga & Navosa, but further placement seems impossible. A numbered Horne specimen from Rambi (*473*) was not listed by Baker. However, he did indicate as a possible representative of the species *Horne 823* (Viti Levu: Namosi), which I now refer to *D. ferrea* var. *gillespiei*.

DISTRIBUTION: The species seems endemic in our area and is clearly indigenous in Fiji, Tonga, and the Horne and Wallis Islands. The only Samoan collection at hand, *Wilder 401*, taken from a small cultivated tree in Apia, is sterile, but Wilder's notes indicate the local name *mapa* and the fact that the fruit, said to measure 40 × 18 mm., is used for scenting oil. From the name it may be assumed that the species was brought to Samoa either from Tonga or the Horne or Wallis Islands.

The species has been noted as a tree 3–15 m. high, the trunk attaining a diameter of 35 cm. or perhaps more, growing in beach thickets or in various types of forest (dense, dry, or open) at altitudes of sea-level to 1130 m. It is sometimes cultivated in villages, presumably for its fruits. The flower-buds and corollas are white or cream-colored and sometimes purple-tinged, and the fruits are yellow to brownish. Throughout its range flowering and fruiting specimens may be found at practically any season.

LOCAL NAMES AND USES: In Fiji the following names, some of which are more or less generic, have been recorded: *kauloa*, *kaukauloa*, *mamba*, *mbamba*, *mbama*, and *mbuka ni singa*. In Tonga and the Horne and Wallis Islands the local name *mapa* seems universal and well known. Uses of the species are many. The hard timber is considered valuable and is often used in house-building. The fruits are widely used to scent oil, and the seeds are frequently noted as edible. In Tonga and the Horne and Wallis Islands the fruits are sometimes used in making leis. In one instance (recorded by Yen for Futuna) the fruits were noted as medicinal, used for infants' mouth infections.

Fiji. YASAWAS: WAYA ISLAND: Nangua, *St. John 18167* (A, BISH, K, UC, US). VITI LEVU: MBA: Mountains near Lautoka, *Greenwood 897* (A, K, NY, UC, US), *897A* (A, BISH, K); Mt. Evans Range, *Greenwood 1278* (BISH, K, NY, UC, US); Naloto Range, *Fiji Dept. Agr. 14781* (BISH, SUVA); vicinity of Tumbenasolo, valley of Namosi Creek, *Smith 4619* (A, BISH, K, US); Mt. Lomalangi (Nanggaranambuluta), *Gillespie 3923* (BISH, UC), *4294* (BISH, K, UC, US); Nandala Valley, *Gillespie 4266* (BISH). NANDRONGA & NAVOSA: *Horne 1013* (K lectotype of *Maba lateriflora*; isolectotype at GH). NAMOSI: Northern slopes of Korombasambasanga Range, in drainage of Wainavindrau Creek, *Smith 8724* (BISH, GH, K, SUVA, UC, US); vicinity of Nanggarawai Village, *Gillespie 3203* (BISH). RA: Vicinity of Rewasa, near Vaileka, *Degener 15388* (A, BISH, K, NY, UC, US), *15415* (A), *15462* (A, NY, US). TAILEVU: Waikombulu Creek, *Berry (E. Damanu) 295* (K, SUVA); Nakalawatha, *Fiji Dept. Agr. 2677* (BISH, SUVA). REWA: Rewa delta, *Tothill 373* (BISH, K). KANDAVU: Mt. Mbuke Levu, *Smith 243* (BISH,

GH, K, NY, UC, US), *Fiji Dept. Agr. 14918* (BISH, SUVA), *14919* (K, MASS, SUVA). OVALAU: Lovoni Valley, *Horne 201* (GH, K); hills near Levuka, *Gillespie 4416* (BISH, K, NY, UC). KORO: Main ridge, *Smith 1045* (BISH, GH, K, NY, UC, US). NGAU: Shore of Herald Bay, vicinity of Sawaieke, *Smith 7893* (BISH, GH, K, SUVA, UC, US). VANUA LEVU: MBUA: Koromba Forest, *Fiji Dept. Agr. 15143* (MASS, SUVA). MATHUATA: Mt. Ndelaikoro, *Fiji Dept. Agr. 13422* (BISH, K, SUVA); Mt. Numbuiloa, east of Lambasa, *Smith 6358* (A, BISH, K, US), *Fiji Dept. Agr. 14624* (BISH, K, MASS, SUVA). THAKAUNDROVE: Maravu, near Salt Lake, *Degener & Ordonez 14208* (A, BISH, K, NY, UC, US). RAMBI: *Horne* (GH, K), *473* (GH, K). TAVEUNI: Vicinity of Wairiki, *Gillespie 4751* (BISH, NY, UC); slopes of Mt. Manuka, east of Wairiki, *Smith 8170* (BISH, K, SUVA, UC, US). KAMBARA: On limestone formation, *Smith 1242* (BISH, GH, K, NY, UC, US). ONGEA NDRIKI: Interior forest, *Bryan 405* (A, BISH, K). FIJI, without further locality: *Tothill 374* (K), *Greenwood 503* (K).

Horne Islands. FUTUNA: Vaisei, *Yen 454* (BISH), *McKee 19773* (BISH, P).

Wallis Islands: UVEA: Inland forest, *Burrows W23* (BISH).

Tonga. VAVA'U: *Crosby 96* (K). LIFUKA: Near southern end of island, *Yuncker 15777* (BISH, US). TONGATAPU: Mua, *Setchell & Parks 15266* (K, UC, US), *15624* (GH, K, UC, US); Ha'ake, *Setchell & Parks 15349* (BISH, K, UC), *15520* (UC); below Niulei Village, south of Nuku'alofa, *Yuncker 15236* (BISH, GH, US). 'EUA: Near center of island, *Yuncker 15355* (BISH, US); Liku terrace, *Parks 16291* (K, NY, UC, US). TONGA, without further locality: *McKern 99* (BISH).

Samoa. UPOLU: Apia, cultivated, *Wilder 401* (BISH).

The taxonomic position of *D. major* is certainly in Section MABA, but it is well differentiated from *D. elliptica* and *D. ferrea* on the basis of its comparatively robust habit and large flowers and fruits. Green (5: 340) correctly indicates that Bakhuizen's concept (2: 442) of *D. ferrea* var. *lateriflora* was too inclusive. Not only is the taxon quite distinct from *D. ferrea*, but from it must be excluded *Maba savaiiensis* Christophersen, a comparatively small-fruited taxon of a very different alliance, which I have discussed above as a well marked variety of *D. elliptica*.

Since in the present treatment the binomial *D. major* is used in place of the long-established *D. lateriflora* and the more recently proposed *D. andersonii*, for a species that is abundant and widespread in our area, a justification is required. The basionym of *D. major* is *Maba major* Forst. f., a binomial based on a fruit observed in Tonga. Forster's description may have called on the brief discussion of "*mabba*" by Captain Cook, quoted above in my consideration of the types of the three competing names. It appears that no specimen was kept to serve as a type for *Maba major*, but this does not detract from the nomenclatural validity of Forster's name. Three taxa of *Diospyros* are known to occur in Tonga, and it is important to decide which one of these was the basis of Forster's and Cook's descriptions.

Diospyros samoensis has a globose to oblate fruit, up to 30 × 30 mm., and the local names in Tonga are *tutuna*, *pekepeka*, *kolivao*, and *kakala'uli*. No notes indicate the edibility of the seed. This species may safely be discarded as a possible candidate for *Maba major*.

Diospyros elliptica var. *elliptica* has an ellipsoid to ovoid fruit no larger

than 20 × 12 mm., and the modern local name in Tonga is *kanume* throughout. A few specimens do indicate that the seed is edible. According to J. R. & G. Forster's original description the native name in Tonga was *maba*; this could have been used as a generic name, or in recording it the Forsters could have had mixed recollections.

There remains the taxon now passing as *D. andersonii*, which has an ellipsoid to ovoid fruit sometimes as large as 60 × 30 mm., and the local name is consistently *mapa* in Tonga, the Horne and Wallis Islands, and Samoa (in cultivation). In Fiji it is often called *mamba* and is sometimes cultivated in villages. Some modern collections note that the seed is edible.

The above data, in reference to the common name, the size of the fruit, and the occasional cultivation, seem to exclude any taxon except *D. andersonii*, which agrees perfectly with the comments provided by both Forster and Cook. In my opinion *Maba major* can no longer be considered a *nomen dubium*, as suggested by Bakhuizen (2: 429), and must be accepted as the oldest basionym for the now well known species *D. andersonii*. It must be admitted that Bakhuizen (2) covered the nomenclatural possibilities for this taxon quite thoroughly. After proposing the combination *D. lateriflora* in 1936, he suggested *D. major* in 1941 with three alternatives: *D. ellipticifolia* var. *major*, *D. major* var. *andersoni*, and *D. ferrea* var. *lateriflora*. These names, which create an involved synonymy, are certainly alternative names in the sense of Art. 34 (Internat. Code Bot. Nomencl. 1966), but since the publication was prior to 1 Jan. 1953 they must be considered valid.

The occasional spelling of the epithet as "*maior*", as by Forster, is corrected to *major* in accord with Art. 73, Note 6, of the Code.

4. **Diospyros christophersenii** Fosberg in Bull. Torrey Bot. Club 65: 613. 1939.

Maba samoensis Hiern in Jour. Bot. 15: 99. *pl. 186.* 1877; Christophersen in Bishop Mus. Bull. 128: 174. 1935; non *Diospyros samoensis* A. Gray.
Diospyros ferrea var. *samoensis* Bakh. in Bull. Jard. Bot. Buitenz. III. 15: 435, 443. 1941.

Tree at least to 6 m. high, the branchlets dark-cinereous, comparatively slender, distally 1.5–3 mm. in diameter, conspicuously lenticellate, glabrous; petioles robust, semiterete, 3–7 mm. long; leaf-blades subcoriaceous, immersed-glandular-punctate, ovate- to oblong-elliptic, 10–21 cm. long, 3.5–8.5 cm. broad, obtuse to subacute at base, narrowed to an obtuse or emarginate apex, the costa sharply impressed above, prominent beneath, the secondary nerves 12–22 per side, spreading, curved, with the veinlet-reticulation raised or prominulous on both sides or plane above; flowering inflorescences not known; fruiting inflorescences axillary or borne on defoliate branchlets, composed of a stout cylindric peduncle 3–6 mm. long and 2–3 mm. in diameter, this with 2 or 3 lateral bract-scars indicating fallen flowers, subpersistently strigose with pale brown hairs 0.2–0.5 mm. long, slightly swollen at apex; fruiting calyx sessile, solitary,

terminal, not conspicuously accrescent, rotate, 9–12 mm. in diameter, strigose without and glabrescent, copiously sericeous within with hairs 0.2–0.5 mm. long, the lobes deltoid, reflexed or spreading, 4–5 × 7–8 mm., obtuse at apex; fruit solitary, oblong-ellipsoid to subfusiform, at maturity 35–40 mm. long and 15–22 mm. broad, often curved, truncate-rounded at base, apically subacute to the stylar base, sparsely strigose with hairs 0.2–0.5 mm. long (but without longer hispidulous indument), tardily glabrate, 2- or 3-locular, the seeds fusiform, triquetrous, 25–33 mm. long.

TYPE LOCALITY: Samoa; the type is *Whitmee 3*, cited below.

DISTRIBUTION: Endemic to Samoa and apparently rare, known with certainty only from Savaii, where Christophersen noted it as a tree 6 m. high growing in wet forest at about 600 m. altitude; his specimen, collected in November, bears fruits that were yellow to slightly orange-yellow.

Samoa. SAVAII: Siuvao-Auala, *Christophersen 3379* (BISH, K, NY, UC, US). SAMOA, without further locality: *Whitmee 3* (K holotype).

As indicated by Bakhuizen (*2*: 435, 442–444), *Maba samoensis* is allied to his concept of *D. ferrea* var. *lateriflora*, but both taxa merit specific status. Hiern's epithet not being available in *Diospyros*, Fosberg correctly proposed a new name. *Diospyros christophersenii* appears to be the Samoan ally of the Fijian-Tongan *D. major*, differing primarily in the indument of its fruit, but also in its comparatively slender branchlets, the more numerous secondary nerves of its leaf-blades, and its slightly longer fruiting peduncles.

Diospyros L. subgen. **Maba** (J. R. & G. Forst.) Bakh. sect. **Rhipidostigma** (Hassk.) Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 370, 382. 1941.

Rhipidostigma Hassk. Retzia **1**: 103. 1855.
Maba sect. *Rhipidostigma* Hiern in Trans. Cambr. Philos. Soc. **12**: 107, 110. 1873.
Diospyros subgen. *Maba* sect. *Hasseltia* Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 9, 10. 1936, 78. 1938.

According to the treatments of Bakhuizen, Sect. RHIPIDOSTIGMA includes four species distributed from southeastern Asia through Malesia to Queensland and New Caledonia; the easternmost of these species has recently been discovered in Fiji.

5. **Diospyros fasciculosa** (F. v. Muell.) F. v. Muell. Austral. Veg. in Intercolon. Exh. Ess. **1866–67**: 35. 1867; Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 78. 1938; P. S. Green in Kew Bull. **23**: 342. 1969.
Maba fasciculosa F. v. Muell. Fragm. Phytogr. Austral. **5**: 163. 1866; Benth. Fl. Austral. **4**: 290. 1868; Hiern in Trans. Cambr. Philos. Soc. **12**: 135. 1873.
Ebenus fasciculosa Kuntze, Rev. Gen. Pl. **2**: 408. 1891.

Tree to 20 m. high, the young parts minutely strigose, the branchlets and foliage soon glabrate, the branchlets slender, obviously lenticellate; petioles semiterete, 5–12 mm. long; leaf-blades subcoriaceous or chartaceous, ovate- or elliptic- or lanceolate-oblong, 5–20 cm. long, 1.5–7 cm. broad, cuneate to subrounded at base and short-decurrent on the petiole, obtuse or obtusely cuspidate at apex, narrowly reflexed at margin, the lateral nerves 7–10 per side, the veinlet-reticulation subimmersed or prominulous beneath; inflorescences axillary, dichotomo-cymose, the staminate 10–25-flowered, branched from base, the branchlets and bracts (ovate, 0.5–1 mm. long) minutely hirtellous-strigose, the pistillate inflorescences more compact, 3- to many-flowered; flowers sessile at apices of ultimate branchlets, the calyx cupuliform or campanulate, 1.5–3 mm. in diameter, minutely strigose and glabrate without, glabrous within, shortly 3-lobed, the lobes obtuse or rounded; corolla campanulate-cylindric, 4–6 mm. long, minutely strigose without and glabrous within, 3-lobed, the lobes ovate, 2–3 mm. long, obtuse; stamens 8–26, slightly unequal, 1.5–2.5 mm. long, the filaments slender, minutely hispidulous, the anthers 1–1.5 mm. long; pistillate flowers essentially similar but sometimes apparently with 4 calyx-lobes, perhaps slightly larger than the staminate, the ovary ovoid, glabrous, 6-locular, each locule 1-ovulate; fruiting calyx cupuliform or campanulate, accrescent, 10–17 mm. in diameter, glabrate, 3- or 4-lobed; fruits subglobose, glabrous, nitid, 7–20 mm. in diameter.

TYPE LOCALITY: In the original publication Mueller lists four specimens from Queensland: Tweed River, *C. Moore*; Brisbane River, *F. v. Mueller*, *W. Hill*; Rockhampton, *Thozet*. The original material is probably deposited in Mueller's herbarium at Melbourne, but apparently some of it is duplicated at Kew. Neither Bentham (1868), Hiern (1873), nor Bakhuizen (1938) have specified a lectotype, but I have not checked all the many other mentions of the species to see if this has been done by another author.

DISTRIBUTION: Bakhuizen (2) records the species from Java, Queensland, and New Caledonia; its occurrence in Fiji was first noted by Green (5). The single available Fijian collection was taken from a tree 12–13 m. high, growing on the edge of forest near sea-level; its white staminate flowers were obtained in January.

Fiji. VATULELE: Nawai, *Fiji Dept. Agr. 13801* (BISH, K, MASS, SUVA).

The interesting discovery cited above, as discussed by Green, extends the range of Section RHIPIDOSTIGMA eastward to Fiji. The species is quite unlike any other species of *Diospyros* known from our area, and its occurrence on the small island Vatulele, off the south coast of Viti Levu, is puzzling. My description is abstracted from Bakhuizen's, with the addition of data from the Fijian collection, which bears staminate inflorescences.

Diospyros L. subgen. **Diospyros.**

The subgenus that includes *D. lotus* L. (Sp. Pl. 1057. 1753) must bear the epithet *Diospyros*. In Bakhuizen's treatment, the species of this alliance in our area fall into *Diospyros* subgen. Eudiospyros (L.) Bakh. sect. Ebenus Bakh. (in Bull. Jard. Bot. Buitenz. III. 15: 19, 32. 1936). Clarification of the sections of *Diospyros* requires the attention of a world-wide specialist on the genus, to whom the appropriate sectional combination in subgen. Diospyros (rather than *Eudiospyros*) may be left.

The species of subgen. Diospyros of our area have had applied to them four epithets: *samoensis*, *vitiensis*, *longisepala*, and *globosa*. In the basic part of his revision Bakhuizen (2) keyed and described only *D. samoensis*, remarking in passing that *D. vitiensis* and *D. longisepala* are doubtless closely allied. In 1939 Fosberg accepted *D. globosa*, and in 1940 he accepted *D. samoensis* in an inclusive sense, reducing *D. vitiensis* outright and proposing varietal status for *D. longisepala*. Bakhuizen, in his "Addenda et Corrigenda" (2), first (p. 407) accepted Fosberg's treatment, but later (p. 457) he reinstated *D. vitiensis*, reducing to it outright *D. longisepala* and *D. globosa*. The last of these treatments appears to me closest to the facts, as good differences between *D. samoensis* and *D. vitiensis* are apparent, although such differences are not emphasized in Bakhuizen's supplementary key (2: 456, 457). The reduction of the type of *D. globosa* to the latter of these concepts (as also pointed out by Green, 5: 340) seems correct. Like Fosberg, I prefer to maintain *D. longisepala* as a variety, but of *D. vitiensis* rather than of *D. samoensis*.

In recognizing two taxa of this relationship at the specific level, it is apparent that foliage and floral characters are not useful. However, *D. samoensis* has its inflorescences, both staminate and pistillate, obviously pedunculate, while in *D. vitiensis* the inflorescences are more congested, often glomerulate. This character is more obviously reflected in fruiting condition: in the former taxon the often solitary fruit is borne on a slender peduncle-branchlet axis 4–15 mm. long, while in the latter the fruit appears subsessile, the supporting peduncle (or branchlet) being stouter and only 2–4 mm. long. An even more dependable difference is noted in the fruiting calyx, which in *D. samoensis* has the limb so abruptly reflexed that a sharp margin of the flattened disk is very obvious; in *D. vitiensis* the limb may be spreading or reflexed, but in this case the angle between the limb and the disk is merely rounded or obtuse.

As thus circumscribed, the two taxa have geographic reality, with an overlap of range only in the Lau Group of Fiji.

Key to Species

Inflorescences pedunculate, the fruits borne on a simple peduncle or a combined peduncle-branchlet axis 4–15 mm. long, this comparatively slender, 1.5–2.5 mm. in diameter, abruptly swollen at apex to 3–5 mm.; fruiting calyx

composed of a conspicuously flattened coriaceous sharp-margined disk 12–17 mm. in diameter, the limb sharply reflexed at an abrupt right angle, the lobes coriaceous but striate with coarse veins, ovate or broadly ovate, slightly broader than long, 5–10 × 7–12 mm., obtuse or rounded at apex. ..... 6. *D. samoensis.*

Inflorescences congested-cymose, often glomerulate, the fruits borne on a simple peduncle (or branchlet) 2–4 mm. long, 2–5 mm. in diameter, gradually swollen toward apex; fruiting calyx composed of a flattened disk 11–15 mm. in diameter, the limb, if reflexed, less sharply so, at less than a right angle, the lobes thick-coriaceous, not striate (venation fully immersed), deltoid to oblong-ligulate, 5–18 × 3–12 mm., subacute to obtuse at apex. ..... 7. *D. vitiensis.*

6. **Diospyros samoensis** A. Gray in Proc. Amer. Acad. Arts **5**: 326. 1862; Hiern in Trans. Cambr. Philos. Soc. **12**: 245. 1873; Drake, Ill. Fl. Ins. Mar. Pac. 230. 1892; Burkill in Jour. Linn. Soc. Bot. **35**: 45. 1901; Christophersen in Bishop Mus. Bull. **128**: 174. 1935; Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 224. 1938, 407. 1941; Fosberg in Bull. Torrey Bot. Club **67**: 417. 1940; Yuncker in Bishop Mus. Bull. **178**: 94. 1943, in op. cit. **184**: 57. 1945, in op. cit. **220**: 214. 1959.

Tree to 25 m. high, the young parts sericeous-strigose, the branchlets terete, soon glabrate, usually obviously lenticellate; petioles semiterete, 3–15 mm. long; leaf-blades chartaceous or thin-coriaceous, opaque, glabrous, ovate-oblong to ovate-elliptic or ovate-lanceolate, 5–20 cm. long, 2.5–9 cm. broad, obtuse to rounded at base, short-acuminate to obtuse at apex, the costa prominent beneath, the lateral nerves 6–10 per side, the veinlet-reticulation prominulous or immersed; inflorescences axillary, cymose, sometimes borne on short defoliate branchlets, short-pedunculate, the staminate 3–13-flowered, pale-strigose or glabrescent, with small deciduous bracts, the flowers sessile on short ultimate branchlets, 4- or 5-merous; calyx campanulate or subcupuliform, 3–5 mm. long and in diameter, strigose without and sericeous within, glabrate; corolla urceolate, 8–15 mm. long, sericeous and glabrate without, glabrous within, the lobes ovate, 2–6 mm. long, obtuse; stamens 8 or 10 (or rarely to 24), free or subfasciculate in pairs, 3–5 mm. long, the rudimentary ovary none or minute and hispidulous; pistillate inflorescences simpler, the peduncle 4–12 mm. long, the flowers usually in threes, sometimes 1 or 2, sessile on the peduncle or on short branchlets; calyx and corolla similar to the staminate, the ovary sericeous, 8- or 10-locular, the ovules solitary; fruiting inflorescences composed of a simple peduncle or an obscurely jointed peduncle-branchlet axis 4–15 mm. long, this slender, usually with a solitary terminal fruit; fruiting calyx accrescent, the tube forming a flattened or depressed-cupuliform disk 12–17 mm. in diameter, this often sericeous within, the limb sharply reflexed at an abrupt right angle, the lobes ovate or broadly ovate, 5–10 mm. long, 7–12 mm. broad, striate with coarse veins, obtuse or rounded at apex; fruit soon glabrate, globose to oblate,

20–30 mm. long, 25–30 mm. broad, the seeds 8 (or perhaps 10), 10–15 mm. long.

TYPE LOCALITY: Samoa; the type, without definite locality other than "Tutuila and Savaii," is a U.S. Exploring Expedition specimen cited below.

DISTRIBUTION: Eastern Fiji (Lau Group), Horne and Wallis Islands, Tonga, Niue, and Samoa. The species is also accredited to the Solomon Islands and New Guinea by Bakhuizen (2: 224), but it is likely that these records should be more carefully examined, since a logical western boundary for the taxon is noted in the Lau Group of Fiji. The species has been noted as a tree 3–25 m. high, with a trunk 8–45 cm. in diameter, occurring in often dry forest, woodland, or thickets, frequently near the sea on limestone but also on overgrown lava fields. Altitudes from sea-level to 600 m. have been recorded. The corolla is white to cream-colored or yellowish white; the fruit is yellow to pink, red, or dark brown, with blackish or dark brown seeds. A vaguely seasonal rhythm is noted in that flowers have been obtained from September to March, fruits from May to November.

LOCAL NAMES AND USES: In Lau the name *kaukauloa* has been recorded, and it is noted that the wood furnishes a hard black "ebony." On Alofi (Horne Islands) the species is known as *kau kau uuli* or *tutunu*, and the wood is used for construction. Common names in Tonga, recorded by Yuncker and other collectors, are *tutuna*, *pekepeka*, *kolivao*, and *kakala'uli*; there the species is used for firewood. On Niue both Yuncker and Sykes indicate the name as *kieto*; the hard black wood is used for spears. Variant names in Samoa are *aoaoli*, *aoauli*, *auaouli*, *au'auli*, and *au'a'uli*, with a single record of *anume* (*Christophersen 1000*); the last more commonly refers to *D. elliptica*.

Fiji. VANUA MBALAVU: Southern limestone section, Malatta, *Smith 1451* (BISH, GH, K, NY, UC, US). FULANGA: In ridge forest, *Bryan 448* (A, BISH, K, UC, US); on limestone, *Smith 1226* (BISH, GH, K, NY, UC, US). ONGEA LEVU: Interior forest and also near sea, *Bryan 430* (A, BISH).

Horne Islands. ALOFI: *McKee 19807* (P), *19822* (BISH, P), *19866* (BISH, P); Mt. Nuku, *Yen X55* (BISH).

Wallis Islands. UVEA: Mt. Afala, *McKee 19921* (P).

Tonga. NIUAFO'OU: *Jaggar*, Oct. 1930 (BISH). VAVA'U: *Crosby 98* (K); below Leimatua, northwest of Neiafu, *Yuncker 16191* (BISH, GH, US); Tuanikavale, *Soakai 765* (K). "VAVA'U and LIFUKA:" *Harvey*, in 1855 (K). KAO: *Yuncker 15967* (BISH, US). TOFUA: Northern side of island, *Scarth-Johnson 162* (K). 'EUA: Near Lokupo, northeastern side, *Yuncker 15521* (BISH, US); above Houma, northwestern side, *Yuncker 15495* (BISH, GH, US), *15496* (BISH, US); Liku terrace, *Parks 16321* (BISH, GH, K, NY, UC, US).

Niue. East of Alofi, *Yuncker 10064* (A, BISH, K, UC, US); Vaipapahi farm, *Sykes 472* (K); Tuhia'atua-Hakupu track, *Sykes 774* (K).

Samoa. SAVAII: Between Aopo and Asau, *Christophersen 3432* (BISH, UC); Tanga, *Christophersen 2821* (BISH, K); Salailua-Lataitai, *Christophersen &*

Hume 2620 (BISH, K, NY, UC, US), *2624* (BISH, UC); Safotu, *Vaupel 483* (BISH, NY), *Christophersen & Hume 2531* (BISH, K, NY, UC, US); Safune, *Christophersen 2396* (BISH, K, US); Matavanu lava field, *Christophersen & Hume 1875* (BISH, US); Neiafu, *Bristol 2203* (BISH); Gataivai, *Bristol 2249* (BISH, K), *2271* (BISH). UPOLU: Falese'ela, Lefaga, *Bristol 2316* (BISH, K); vicinity of Apia, *Reinecke 107* (BISH, K, US), *Eames 121* (BISH, NY); Lanutoo, *Christophersen 387* (BISH, K, NY); Vaea Mt., *Christophersen 465b* (BISH, NY); below Malololelei, *Christophersen 291* (BISH, UC, US). TUTUILA: Papatele ridge, *Christophersen 1000* (BISH, K, NY, UC); vicinity of Pago Pago, *Diefenderfer 16* (BISH); Fagasa trail, *Setchell 63* (UC); trail to Vatia, *Setchell 333* (BISH, UC, US); road to Nuuuli Village, *Yuncker 9378* (BISH, UC, US); Breakers Pt., *Wisner 121* (BISH). OFU: Toanga, *Garber 1095* (BISH); Nuu islet, *Garber 1103* (BISH, US); southeast shore trail, *Yuncker 9514* (BISH, K), *9516* (BISH). SAMOA, without further locality: *U.S. Expl. Exped.* (US 67253 & 67254 holotype; isotypes at K, NY), *Horne* (GH, K), *Whitmee 20* (K).

The overly inclusive nature of some past interpretations of *D. samoensis* has been discussed above in my comments on Subgenus DIOSPYROS. In fact, this species is sharply demarcated from its closest ally, *D. vitiensis*, and has a very natural distribution.

7. **Diospyros vitiensis** Gillespie in Bishop Mus. Bull. 74: 14. *fig. 17.* 1930; Bakh. in Bull. Jard. Bot. Buitenz. III. 15: 457. 1941.

Tree 3–15 m. high, the young parts minutely strigose, the branchlets and foliage very early glabrate, the branchlets terete, usually copiously and conspicuously lenticellate; petioles semiterete, 3–14 mm. long; leaf-blades chartaceous or subcoriaceous, glabrous, often punctulate-glandular, ovate-oblong or elliptic or elliptic-lanceolate, 7–18 cm. long, 3.5–12.5 cm. broad, obtuse to cuneate at base, obtusely short-acuminate at apex, the costa prominent beneath, the lateral nerves 5–10 per side, usually conspicuous at least beneath, the veinlet-reticulation prominulous or immersed; inflorescences axillary, congested-cymose, the staminate short-pedunculate or glomerulate and short-branched from base, 3–10-flowered, pale-sericeous, the bracts deltoid, about 1 mm. long; calyx 3- or 4-lobed, sparsely strigillose without and soon glabrate, about 4 mm. long and in diameter, the lobes broadly ovate, apiculate; corolla cylindric-urceolate, 10–12 mm. long, the lobes 3 or 4, ovate-deltoid, obtuse; stamens 15–20, free or fasciculate in pairs, 3–6.5 mm. long, the anthers somewhat longer than the filaments; rudimentary ovary minute, glabrous; pistillate inflorescences simpler, the flowers 1–3 and 4- or 5-merous, similar to the staminate or the corolla somewhat shorter and broader, the ovary soon glabrate; fruiting inflorescences axillary or borne on defoliate branchlets, composed of 1 or 2 simple peduncles (or branchlets) 2–4 mm. long and 2–5 mm. in diameter, these gradually swollen toward apex, the fruit solitary, terminal; fruiting calyx accrescent, glabrous, the tube forming a flattened disk 11–15 mm. in diameter, the limb spreading or reflexed, the lobes thick-coriaceous, 4 or 5 (very rarely 3), deltoid to oblong-ligulate, 5–18 mm. long, 3–12 mm. broad, subacute to obtuse at apex; fruit soon

glabrate, ellipsoid to obovoid to globose or oblate, 20–40 mm. long, 20–30 mm. broad, the seeds usually 8, about 15 mm. long.

Although in my observation this species is a Fijian endemic, Bakhuizen (2: 457) cites in the synonymy, with question, *D. acris* Hemsl. (in Kew Bull. **1895**: 136. 1895), typified by *Comins 311*, from the Torres Islands, New Hebrides. At the moment no evidence indicates the advisability of giving up the Fijian binomial for Hemsley's older one. Points of separation between *D. vitiensis* and *D. samoensis* are discussed above.

I have not discovered a reliable means of separating the two suggested varieties of *D. vitiensis* in the absence of mature fruits, but the extremes of the fruiting calyx are such that it seems inadvisable to ignore them. Fortunately specimens of *Diospyros* are more often collected in fruit than in flower. It must be acknowledged that the fruiting calyces are somewhat variable on a few collections, and some of these have been referred to one or the other variety without much conviction. The type of *D. globosa*, with staminate flowers, is referred to var. *longisepala* because another Kambara collection, *Smith 1272*, has obviously elongate fruiting calyx-lobes. Future material from Lau will hopefully indicate whether only var. *longisepala* occurs there.

KEY TO VARIETIES

Calyx-lobes associated with mature fruit reflexed, deltoid, often about as broad as long, 5–10 (–12) mm. long, 5–12 mm. broad at base. . . . 7a. var. *vitiensis*.

Calyx-lobes associated with mature fruit spreading or reflexed, oblong-ligulate or deltoid-oblong, conspicuously longer than broad, 8–18 mm. long, 3–10 mm. broad at base. . . . . 7b. var. *longisepala*.

7a. Diospyros vitiensis var. vitiensis.

Diospyros vitiensis Gillespie in Bishop Mus. Bull. **74**: 14. *fig. 17*. 1930.

Diospyros samoensis var. *longisepala* sensu J. W. Parham, Pl. Fiji Isl. 161. quoad *fig. 61, A* (err. legend as *B*), non sensu typi. 1964.

The typical variety, characterized by having the calyx-lobes associated with the mature fruit reflexed, deltoid, often about as broad as long, 5–10 (–12) mm. long, 5–12 mm. broad at base.

TYPE LOCALITY: Province of Namosi, Viti Levu, Fiji: the type is *Gillespie 3083*, cited below.

DISTRIBUTION: Endemic to Fiji, and known definitely only from Viti Levu and Vanua Levu, where it has been noted as an often slender tree 3–15 m. high in dense, dry, or secondary forest at altitudes of 100–1120 m. The fruit is greenish yellow to dull yellow, becoming yellowish brown or brown. Fruiting specimens have been obtained between May and December.

LOCAL NAMES: *Kauloa, mbaumbulu, mbulumate, mbole.*

Fiji. VITI LEVU: MBA: *Fiji Dept. Agr. 14468* (BISH, SUVA): northern slopes of Mt. Namendre, east of Mt. Koromba, *Smith 4543* (A, BISH, K, US); vicinity

of Nandarivatu, *Gillespie 4207* (BISH, UC), *Fiji Dept. For. 262* (*Watkins 784*) (K, SUVA); hills between Nggaliwana and Nandala Creeks, *Smith 5817* (A, BISH, K, US); vicinity of Nandala, *Degener 14835* (A). NANDRONGA & NAVOSA: Northern portion of Rairaimatuku Plateau, between Nandrau and Rewasau, *Smith 5446* (A, BISH, K, US). SERUA: Hills between Wainiggere and Waisese Creeks, between Ngaloa and Wainiyambia, *Smith 9379* (BISH, GH, K, SUVA, UC, US); hills east of Navua River, near Nukusere, *Smith 9086* (BISH, GH, K, SUVA, UC, US); Navua River near Namata Rapids, *Gillespie 2950* (BISH). NAMOSI: Mt. Naitarandamu, at Navunitaruilau, on wooded ridge between the watersheds of the Wainimala and the Wainikoroiluva, alt. 900 m., Sept. 27, 1927, *Gillespie 3083* (BISH holotype; isotypes at K, NY, UC, US); east of Namosi Village, *Gillespie 2829* (BISH, UC). VANUA LEVU: MATHUATA: Nakoroutari, *Fiji Dept. Agr. 15239* (BISH, K, SUVA). THAKAUNDROVE: Hills between Vatukawa and Wainingio Rivers, Ndrekeniwai Valley, *Smith 584* (BISH, GH, K, NY, UC, US); hills west of Korotasere, Natewa Bay region, *Smith 1946* (BISH, GH, K, NY, UC, US).

7b. **Diospyros vitiensis** var. **longisepala** (Gillespie) A. C. Sm., comb. nov.

Diospyros longisepala Gillespie in Bishop Mus. Bull. **74**: 14. *fig. 16*. 1930.
Diospyros samoensis var. *longisepala* Fosberg in Bull. Torrey Bot. Club **67**: 418. 1940; Bakh. in Bull. Jard. Bot. Buitenz. III. **15**: 407. 1941; J. W. Parham, Pl. Fiji Isl. 162, excl. *fig. 61, A*. 1964.
Maba globosa A. C. Sm. in Bishop Mus. Bull. **141**: 121, sensu typi, excl. *fig. 63*. 1936.
Diospyros globosa Fosberg in Bull. Torrey Bot. Club **65**: 612. 1939; J. W. Parham, Pl. Fiji Isl. 160. 1964.

Scarcely separable from the typical variety in foliage or flowers, but characterized by having the calyx-lobes associated with the mature fruit often spreading, sometimes reflexed, oblong-ligulate or deltoid-oblong, conspicuously longer than broad, 8–18 mm. long, 3–10 mm. broad at base.

TYPE LOCALITY: Mba Province, Viti Levu, Fiji; the type is *Gillespie 4360*, cited below. The type of *Maba globosa* is *Smith 1241*, cited below, from the island of Kambara in Lau.

DISTRIBUTION: Endemic to Fiji, and thus far known from several islands, apparently being more widespread than var. *vitiensis*. This variety has been recorded as an often slender or spreading tree 3–10 m. high, occurring from sea-level to 970 m. in various types of forest, sometimes on limestone. The corolla is noted as white and the fruit as greenish yellow; flowers have been obtained in March and fruits more or less throughout the year.

LOCAL NAMES: *Kaukauloa, kailoa, mbama, mulu, sawira.*

Fiji. YASAWAS: WAYA ISLAND: North of Yalombi, along Olo Creek, *St. John 18121* (A, BISH). VITI LEVU: MBA: Mt. Evans Range, *Greenwood 444* (K), *954* (A, BISH, K, NY, UC), *1253* (A, BISH, K, NY, UC, US); Mt. Mbatilamu, *Fiji Dept. Agr. 14810* (BISH, SUVA), *14812* (BISH, SUVA); Nandendeleva, *Fiji Dept. Agr. 14851* (BISH, K, MASS, SUVA); Savundamatau Creek, west of Nandarivatu,

Webster & Hildreth 14255 (DAV, MASS); southern slopes of Mt. Ndelainathovu, on escarpment west of Nandarivatu, *Smith 4943* (A, BISH, K, US); slopes of Mt. Lomalangi (Nanggaranambuluta), near Nandarivatu, alt. 950 m., Dec. 20, 1927, *Gillespie 4360* (BISH holotype); hills between Nandala and Nukunuku Creeks, along trail from Nandarivatu toward Lewa, *Smith 6200* (A, BISH, K, NY, US); Nandala, *Degener 14741* (A, BISH, K, NY, UC, US). NANDRONGA & NAVOSA: *Horne 904* (K); Nausori Highlands, *Fiji Dept. Agr. 12649* (A, K, SUVA). NAITASIRI: Nanggarathangithangi, Mendrausuthu Range, *Fiji Dept. Agr. 15028* (MASS, SUVA). OVALAU: Hills west of Lovoni Valley, on ridge south of Mt. Korolevu, *Smith 7631* (BISH, GH, K, SUVA, UC, US); Lovoni Valley, *Horne 195* (GH, K), *Fiji Dept. Agr. 14504* (BISH, SUVA). NGAU: Hills east of Herald Bay, inland from Sawaieke, *Smith 7775* (BISH, GH, K, SUVA, UC, US). VANUA LEVU: MBUA: Upper Ndama River valley, *Smith 1608* (BISH, GH, K, NY, UC, US). KAMBARA: On limestone formation, in forest, alt. 0–100 m., *Smith 1241* (BISH holotype of *Maba globosa*; isotypes at GH, K, NY, UC, US); same locality, *Smith 1272* (BISH, GH, K, NY, UC, US).

CULTIVATED SPECIES

8. **Diospyros discolor** Willd. Sp. Pl. 4(2): 1108. 1806; Hiern in Trans. Cambr. Philos. Soc. 12: 260. 1873; Bakh. in Bull. Jard. Bot. Buitenz. III. 15: 145. 1938.

Samoa, without further locality: *Guest 5* (BISH).

The cultivated occurrence of *D. discolor* in our area is indicated by a single sterile specimen. The species, placed by Bakhuizen in his subgen. EUDIOSPYROS sect. EBENASTER, is endemic to the Philippines, now widely cultivated for its edible fruit, usually with the common name *mabolo*.

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THE GENERA OF OROBANCHACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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OROBANCHACEAE Ventenat, Tabl. Règne Vég. 2: 292. June 1799, "Orobanchoideae," nom. cons.
(BROOMRAPE FAMILY)

Annual or perennial, root-parasitic, achlorophyllous herbs, often fleshy, with 1 to several flowering shoots arising from a more or less thickened base,[2] pubescent with glandular or sometimes also nonglandular hairs. Leaves reduced to scales, alternate, the upper passing imperceptibly into bracts. Inflorescence racemose or spicate, or flowers rarely solitary. Flowers perfect, zygomorphic, hypogynous, axillary to bracts, with or without bractlets, long-pedicelled to sessile. Calyx persistent, synsepalous, nearly actinomorphic to strongly zygomorphic, with 1–5 lobes or teeth. Corolla sympetalous, tubular, the limb mostly 2-lipped, the upper lip 2-lobed to entire, the lower usually 3-lobed. Androecium of 4 didynamous stamens inserted on the tube of the corolla and alternate with its lobes; filaments elongate to very short, included or exserted; anthers dorsifixed, with placentoids, 4-sporangiate, bilocular at maturity, the locules dehiscing lon-

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants of this area, with supplementary information in brackets. References that I have not seen are marked by an asterisk. The literature of Orobanchaceae, especially of those genera important as parasites of crop plants, is vast. The literature lists given in this paper by no means claim to be exhaustive.

I am indebted to Dr. Wood for his careful review of the manuscript and for other aid always so unstintingly given; to Dr. B. L. Burtt for comments on parts of the manuscript; to Dr. Y. D. Tiagi for an English summary of his 1962 Russian paper on floral anatomy of certain Orobanchaceae and Scrophulariaceae and for permission to quote from this summary; and to the curators of the herbaria who responded to my request for data on and specimens of southeastern Orobanchaceae. The illustrations were made by Virginia Savage (FIGURE 1), and by Sydney B. Devore and Diane C. Johnson (FIGURE 2) from dissections by Dr. Wood. Specimens for the illustrations were collected for the Generic Flora of the Southeastern United States by Dr. Wood and Dr. K. A. Wilson, Mr. R. J. Eaton, and myself.

[2] I am aware of no acceptable (to me) morphological term to apply to the swollen base of the plant of *Epifagus* or *Orobanche* or to that — seemingly quite different — of *Conopholis*. For terms such as "tuber," "tubercle," and "gall," my enthusiasm knows bounds.

gitudinally; pollen triaperturate or rarely nonaperturate. Gynoecium syncarpous, the carpels 2 or rarely 3; stigma simple, variable, often capitate, crateriform, or bilamellate; style single, elongate, included or exserted; ovary usually unilocular, with 4 or rarely 5 or 6 [2 or 3] parietal placentae; ovules many, unitegmic, tenuinucellar, mostly anatropous; embryo sac development normal (Polygonum type); endosperm *ab initio* cellular, with terminal haustoria. Fruit a 2- or rarely 3-valved capsule, typically dehiscing anteroposteriorly, the valves usually lateral, each bearing 2 [1] placentae; seeds numerous, endospermous, with a minute undifferentiated embryo. TYPE GENUS: *Orobanche* L.

The Orobanchaceae comprise about 150 species in 17 genera (14 recognized by Beck-Mannagetta; three — *Mannagettaea*, *Necranthus*, and *Tienmuia* — described since). In the conterminous United States four genera occur; three of these, represented by four species, are found in the Southeast.

A majority of the genera and about 90 per cent of the species of Orobanchaceae are native to the Old World. *Conopholis*, *Epifagus*, and *Kopsiopsis* are confined to the New World; *Boschniakia* and *Orobanche* are native in both hemispheres. The family is primarily one of the North Temperate and warm zones. Only about 10 per cent of the species occur in the tropics; only one species reaches the arctic.

Orobanchaceae are one of only about a dozen families of angiosperms in which the parasitic habit is known. They are the largest family of holoparasitic flowering plants. The range of hosts is large, including both woody and, more commonly, herbaceous species; both gymnosperms (rarely) and angiosperms; monocots and dicots. Reports of Orobanchaceae on ferns require verification. Some Orobanchaceae are confined to a single host species or genus; at the other extreme, some parasitize many species and genera, especially Compositae, Labiatae, and Leguminosae.

One earlier worker (Wiesner) claimed to have detected chlorophyll in *Orobanche*, but modern studies, utilizing electron microscopy (Laudi; Laudi & Albertini) and chromatography (Baccarini & Melandri; cf. *Orobanche*) found this pigment to be completely lacking in *Orobanche* and *Lathraea*. There seems little doubt that Orobanchaceae are achlorophyllous.

It is generally assumed that seeds of Orobanchaceae germinate only in the presence of stimulants produced by roots of the host plant — a phenomenon of obvious advantage to the parasite. However, the need for host-stimulants has been demonstrated only in *Orobanche*; such work remains to be done with other orobanchaceous genera. In *Orobanche*, not one but a complex of substances is involved. Some of these have been characterized chemically, but their structure is undetermined. Production of the substances is most active in that region of the root apex where the cells are undergoing and completing their growth in length. The substances may diffuse into the soil for a distance in excess of 1 cm. It would appear that many *Orobanche* seeds within this zone of diffusion

are stimulated to germinate but are unable to form a parasitic attachment because their radicles usually do not exceed 2 mm. in length. The "axiom" that host-stimulants are always required for germination of *Orobanche* seeds was recently called into question by Krenner, who reported that *fresh* seeds of *O. cumana* germinated in plain water in fair numbers. After overwintering, however, the seeds germinated only in the presence of host root exudates.

The embryo of members of the Orobanchaceae is quite undifferentiated and may consist of as few as 45 cells. Its proximal end gives rise to the radicle. After germination of the seed and subsequent penetration of the host by the primary haustorium, the part of the seedling outside the host root enlarges to form the small, so-called "tubercle." At the apex of the "tubercle," which corresponds to the distal end of the embryo, is the plumule. From the proximal part of the "tubercle" secondary roots may arise. Continued enlargement of the "tubercle" — often incorporating tissues of the host, which are stimulated to abnormal growth — may result in a large, rather regularly shaped "tuber" (e.g., *Epifagus*) or in a large, misshapen "tuber" (e.g., the "gall" of *Boschniakia* and *Conopholis*). The "tubercle" in some species enlarges but little, the bulk of the subterranean part of the plant being secondary roots.

Parasitic haustoria in Orobanchaceae are of two kinds. The primary haustorium, terminal in origin, develops from direct transformation of the radicle after it reaches the host root. Secondary haustoria arise laterally from secondary roots of the parasite following contact of these roots with those of the host. Secondary roots do not always bear haustoria. There is no evidence of phloem in the haustoria, the vascular systems of host and parasite being connected by a slender strand of xylem that is sometimes irregular or even double (Kuijt). In *Orobanche*, many of the distal cells of the primary haustorium are said to be multinucleate.

The roots of *Orobanche* are exogenous, but "they are unmistakably roots" (Kuijt). In contrast, those of *Epifagus* are endogenous. *Conopholis* produces no roots.

The gynoecium of most Orobanchaceae (the "Orobanchaceae bicarpellatae" of Beck-Mannagetta), including those of southeastern United States, has traditionally been interpreted as consisting of two carpels, with each carpel bearing two placentae displaced from the margin toward the midline of the carpel. Accordingly, each of the resulting four placentae is the product of but one carpel. That *Orobanche* has *four* carpels was first suggested by B. Tiagi & Sankhla, then denied by Guédès in a reaffirmation of the traditional interpretation of the gynoecium, and finally defended and elaborated upon by Y. D. Tiagi. According to Tiagi, *Orobanche* has four carpels, two median and two lateral; each carpel bears a placenta along each margin. The marginal placentae of adjacent carpels are fused, and thus the ovary contains four placentae, each the product of two carpels. Dr. Tiagi interpreted in exactly the same way the gynoecium of *Conopholis*, FAA-preserved specimens of which I sent to him. The gynoecium of *Epifagus* is basically identical to that of *Conopholis* and

Orobanche and so would certainly be regarded by Tiagi as four carpellate also.

Two lines of gynoecial evolution in the Orobanchaceae are recognized by Y. D. Tiagi. In one line, exemplified by *Boschniakia*, the number of carpels is reduced from four to two. In the other line, exemplified by *Aeginetia*, *Cistanche*, and *Orobanche*, all four carpels are retained, but the lateral ones are smaller and are devoid of midrib bundles. It is unfortunate that Tiagi's scheme does not account for those species of Orobanchaceae (the "Orobanchaceae tricarpellatae" of Beck-Mannagetta) that have six placentae. Are these six-carpellate?

The relationships of Orobanchaceae are controversial. Three points of view are held: the broomrapes are most closely related to the (1) Scrophulariaceae, (2) "Solanaceae and allied taxa" (Y. D. Tiagi), and (3) Gesneriaceae. Also questioned is the maintenance of Orobanchaceae as a separate family.

The majority of workers favors a close relationship between Orobanchaceae and Scrophulariaceae. Boeshore concluded that these taxa form a continuous morphological and physiological series "from non-parasitic through semi-parasitic Scrophulariaceae to the most degraded parasites of the family [e.g., *Striga orobanchoides*, *Harveya*, *Hyobanche*], and that these again show direct continuity with the still more degraded and condensedly parasitic types of Orobanchaceae" and that the Orobanchaceae and Scrophulariaceae, "alike logically and biologically . . . should be treated in continuous descending series from the highest to the most degraded genera."

After a study of the stomatal apparatus of various heterotrophic flowering plants, Linsbauer & Ziegenspeck concluded that *Orobanche* is the culmination of an evolutionary series beginning with nutrient-salt parasites, such as *Striga*, among the Scrophulariaceae-Gerardieae [Buchnereae].

On embryological grounds, relationship between Orobanchaceae and Scrophulariaceae was first suggested by Schnarf. Several years later Glišić pointed out that the two families are so similar embryologically that they could well be united. More recently, B. Tiagi (1963) concluded, again on the basis of embryology, that the Orobanchaceae are "derived from the family Scrophulariaceae (Rhinanthoideae) through forms like *Striga orobanchoides*."

In anther structure, certain Orobanchaceae and certain parasitic Scrophulariaceae are similar in that one longitudinal half of the anther has become reduced or otherwise modified. Some of these genera were placed by Livera in his proposed family Aeginetiaceae, distinguished mainly by characteristics of the anthers: "Of the two anther cells [i.e., halves] one only is fertile, the other either wanting . . . or in the form of a spur. . . ." Kuijt suggested that, on the basis of anther evolution and "other evolutionary trends, there appear to be no serious objections to the possibility that *Christisonia*, and perhaps even *Aeginetia* [both of the Orobanchaceae], are derivatives of *Harveya* [Scrophulariaceae]. Should this conception be

valid, the familial status of Orobanchaceae would be further undermined." Nikiticheva found the similar development of microspores and pollen in Orobanchaceae and in certain parasitic Scrophulariaceae particularly striking.

Gynoecial differences are the traditional ones separating Orobanchaceae and Scrophulariaceae, the former having a unilocular ovary with parietal placentae, the latter, a bilocular ovary with axile placentae. Locule number is, however, not an infallible characteristic. Species of *Christisonia* (including *Campbellia*) of the Orobanchaceae may have either a unilocular or bilocular ovary; in at least one species the ovary is bilocular below and unilocular above. Among the Scrophulariaceae a few genera (*Dopatrium*, *Limosella*, *Micranthemum*) have unilocular or imperfectly bilocular ovaries. Members of *Lathraea*, a genus that has been shifted back and forth between Orobanchaceae and Scrophulariaceae, have unilocular ovaries. Arekal reported a tendency toward unilocularity in the distal portion of the ovary of the scrophulariaceous genera *Orthocarpus* and *Aureolaria* ("*Gerardia*") and concluded that a clear transition from the two-celled [two-locular] ovary of most Scrophulariaceae to the one-celled [one-locular] ovary of Orobanchaceae exists. Levyns found the ovary of *Hyobanche*, a genus of South African Scrophulariaceae, to be imperfectly bilocular, with axile placentation below and parietal above; considering that this "discovery . . . breaks down the principal character separating the families," she included Orobanchaceae in Scrophulariaceae. (The two families had been combined even earlier by Bellini and by Hallier.)

That placentation in Orobanchaceae and Scrophulariaceae is fundamentally different was recently questioned by Y. D. Tiagi, who concluded that in these families placentation is anatomically the same. In *Veronica longifolia* and other Scrophulariaceae studied by him, he found the placentae to be so close together as to appear united, thus making the ovary bilocular, but the placentae were only connivent, each having its own epidermis. In some flowers a gap could be seen between the placentae. Tiagi concluded that placentation in both Orobanchaceae and Scrophulariaceae is parietal.

According to Y. D. Tiagi, "the occurrence of a fundamentally tetracarpellary gynoecium in the family Orobanchaceae must rule out any suggestion of its origin from the Scrophulariaceae," which "have a uniformly bicarpellary gynoecium."[3] The similarities between "Orobanchaceae and certain of the Scrophulariaceae can be more logically considered as examples of parallel evolution rather than indicative of relationships. Search for the ancestors of the Orobanchaceae may be better made among the Solanaceae and allied taxa where the multicarpellary condition of the gynoecium is quite often met with."

[3] The Scrophulariaceae would perhaps be better characterized as "almost" uniformly bicarpellary. The South African genus *Bowkeria* apparently can be tricarpellary: Phillips (Gen. So. Afr. Fl. Pl. 669. 1951) describes the ovary as "2–3 chambered" and the capsule as having "3 or 2" valves.

The Orobanchaceae, because of their typically unilocular ovary, have been included by some authors (e.g., Baillon, Eichler, and Warming) as a parasitic offshoot of the Gesneriaceae. The idea of close relationship between these two families has been revived by Crété, who asserted that embryologically the Orobanchaceae and Scrophulariaceae do not have "direct affinities" but that the broomrapes are so closely related to the Gesneriaceae that they could well be united with them. The Orobanchaceae seem especially similar to Gesneriaceae in their accumulation of orobanchin, in their lack of aucubin-like glucosides, and in their high silicic acid content (Hegnauer).

The biology of most Orobanchaceae — their ecology, morphology, development, host relationships, longevity, pollination, dispersal, etc. — is not well known. Even such basic information as host plant is seldom determined and noted by collectors. Orobanchaceae, because of discoloration and brittleness, usually make rather unpleasing exsiccata. The discoloration, at least in *Orobanche*, has been attributed to the oxidation of orobanchoside, a glucoside.

Cleistogamy in the family appears to be a regular feature only in *Epifagus* although subterranean cleistogamous flowers have been reported in *Cistanche*. Peloric flowers are known to occur in *Orobanche*.

Orobanchaceae, especially *Aeginetia* and *Orobanche* but also *Christisonia*, are of economic importance primarily as parasites of various crop plants. A few species are used in folk medicine.

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KEY TO THE GENERA OF OROBANCHACEAE IN THE SOUTHEASTERN UNITED STATES

General characteristics: *root parasites lacking chlorophyll; leaves scale-like, crowded to clearly alternate; flowers sympetalous, zygomorphic; stamens 4, epipetalous; ovary superior, 1-locular, with 4 parietal placentae, each bearing many anatropous ovules; fruit capsular; embryo minute, undifferentiated.*

A. Flowers in large part with calyptriform corollas, cleistogamous, sometimes a distal few tubular and chasmogamous. ..... 1. *Epifagus*.

A. Flowers all with tubular corollas, chasmogamous.

B. Flowers bibracteolate; calyx split anteriorly, "spathaceous"; stamens exserted. ..... 2. *Conopholis*.

B. Flowers ebracteolate; calyx split anteroposteriorly or campanulate and 5-cleft to 5-parted; stamens included. ..... *3. Orobanche.*

1. **Epifagus** Nuttall, Gen. N. Am. Pl. 2: 60. 1818, nom. cons.[4]

Low, puberulent or glandular-puberulent, yellow, black-purple, purple-brown, yellow-brown, or brown, simple or branched annuals. Base of plant an enlarged "tuber" bearing leaf-scales and thick, short, coralloid, usually branched secondary roots. Stem with scattered, alternate leaf-scales. Inflorescence racemose, each flower bibracteolate, short pedicelled. Calyx obliquely broadly campanulate, nearly equally 5-toothed to 5-lobed. Cleistogamous flowers: usually fertile; corolla calyptriform, persistent for a time on the enlarging capsule, 4-lobed, the upper lobe internal, entire to slightly notched; stamens included, the filaments very short, the anthers at first free but becoming hard and firmly adnate to the stigma, anther halves somewhat divergent, mucronulate basally, those of adjacent stamens becoming connate; style declined anteriorly, very short, included; stigma capitate, slightly bilobed; style, stigma, corolla, and stamens deciduous as a unit. Chasmogamous flowers: usually sterile; corolla tubular, somewhat laterally compressed, usually slightly arcuate, often widening distally, soon deciduous, 4-lobed, the upper lobe internal, erect, rounded, entire or slightly notched, the lower lobes erect to somewhat spreading, acute; stamens included to slightly exserted, the filaments elongate, anthers free, anther halves somewhat divergent, mucronulate basally; style elongate, soon deciduous, usually exserted; stigma capitate, slightly bilobed. Capsule somewhat compressed laterally, thickest below the middle, more or less reniform in lateral view but with a truncate base, 2-valved or rarely 3-valved, dehiscing anteroposteriorly. Seeds minute, very numerous, narrowly ovoid to ellipsoid; testa finely reticulate. (*Leptamnium* Raf.) TYPE SPECIES: *E. americanus* Nutt., nom. illeg. = *E. virginiana* (L.) Bart. (*Orobanche virginiana* L.). (Name from Greek, *epi*, upon, and Latin, *fagus*, beech, in allusion to the host plant.) — BEECHDROPS, CANCER-ROOT.

A genus of one North American species. *Epifagus virginiana* (L.) Bart. (*Leptamnium virginianum* (L.) Raf.), beechdrops, ranges from Cape Breton and Prince Edward islands south to northern Florida and west to eastern Texas, Arkansas, southeastern Missouri, southern Illinois, Indiana, eastern Wisconsin, and the upper peninsula of Michigan. Isolated occurrences, separated from the main range by at least 550 miles, are in the highlands of Tamaulipas and Hidalgo. The ranges of beechdrops and its host trees, American beech (*Fagus grandifolia* var. *grandifolia*), and Mexican beech (*F. grandifolia* var. *mexicana*), are more or less identical, although beechdrops has not yet been found in Oklahoma or in Puebla. *Fagus grandifolia* was not reported from Mexico until 1939; *Epifagus*, not until 1950. These species share, with a number of others, a charac-

[4] Conservation superfluous; see Rickett & Stafleu, Taxon 9: 113. 1960.

FIGURE 1. **Epifagus.** a–k, *E. virginiana*: a, plant with fruits, cleistogamous flowers, and buds, × 1/3; b, base of plant, showing coralloid roots below, leaf-scales with buds or branches above — note portion of small root of *Fagus* to which plant is attached, × 1; c, tip of flowering branch with chasmogamous flowers above and two cleistogamous ones below, the lowermost flower with partly developed fruit, the corolla already fallen, × 1; d, chasmogamous flower, × 5; e, same, with half of calyx and corolla and two stamens removed — note nectary at base of ovary on abaxial side, × 5; f, diagrammatic cross section of ovary, showing placentation, × 10; g, cleistogamous flower, the calyptriform corolla being pushed off by growth of ovary, × 5; h, same, in vertical section — note developing seeds, × 5; i, nearly mature fruit seen from abaxial side, × 5; j, open capsule with seeds, abaxial side at left, × 5; k, two seeds, × 40.

teristic bicentric distribution pattern: eastern United States and the highlands of eastern Mexico. The distribution of these may have been continuous during the early Pleistocene, a controversial matter. Decreased rainfall in Texas and northeastern Mexico later may have brought about the present disjunction.

Although it has been suggested that *Epifagus* is saprophytic (Hill) or that it is "self-sustaining after an initial period of parasitism" (Meehan), the plant is certainly an obligate parasite during its entire life. Connection with a beech root is demonstrable regardless of the age of the parasite. Such connection is to roots mostly 1 to 3 mm. thick. It is most easily broken unless extreme care is taken in excavating the beechdrops plant (and often in spite of such care). Beechdrops withers and dies quickly if a trough is dug around it to sever the parasitized root. Parasitic union, made with beeches of all ages (even one-year-old seedlings), is effected by means of a primary haustorium that pierces the beech root (Brooks). Earlier workers (Cooke & Schively) had reported that the organ of connection between beech and beechdrops arises from the beech and grows into the tissues of the parasite. As the beechdrops tuber grows, its tissues develop around the beech root, which eventually becomes buried therein. No secondary haustoria are formed.

Beechdrops is usually purple-brown, but variant color forms occur; butter-yellow (Palmer), black-purple (forma *atropurpurea* Pease), and pale brown (forma *pallida* Weatherby). The purple-brown color is soluble in alcohol, the plant becoming bleached but the alcohol darkening.

The mature plant is differentiated into two regions: an enlarged base, the "tuber," and an aërial "stem," the inflorescence. The "tuber" is considered by Boeshore to represent a "fused primary root below and a greatly condensed vegetative stem-axis above." The curious, short, branching coralloid roots are generally more common on, and may be confined to, the lower part of the "tuber," which also may bear some scale-leaves between the roots. The roots may be tightly appressed to those of beech but form no parasitic attachment. Their primary function may be one of support — they are more numerous in loose soil than in firm. The upper portion of the "tuber" bears scale-leaves. A swelling, perhaps representing an abortive branch, is generally found in the axil of each scale. Some roots may be present between the scales. Apically the "tuber" narrows into the aërial "stem," which may reach 1/2 meter in height. The inflorescence is usually branched but may be simple. All branches are axillary to scale-leaves. Some additional branches may arise from the apex of the "tuber."

Stomata are abundant and widespread on the aërial parts, even including the style. The rapid wilting of beechdrops after it is severed from the host root is probably due largely to excessive transpiration through the numerous stomata.

Cleistogamous flowers are the first to appear and are usually more numerous than chasmogamous ones. They may even develop underground. Some plants, or even whole colonies, may bear no chasmogamous

MAP 1. Documented distribution of *Epifagus virginiana*. Inset shows northeastern Mexico and southern Texas. For distribution of *Fagus grandifolia* see Jour. Arnold Arb. **52**: 169. 1971.

flowers. When produced, these flowers are proterogynous and are distal on the branches that have been producing cleistogamous flowers. Above the chasmogamous flowers one to several cleistogamous flowers usually occur. The two types of flowers are often connected by some of intermediate morphology. Cleistogamous flowers generally are followed by good fruits, and chasmogamous flowers are not, but exceptions occur.

In young cleistogamous flowers the anthers are free from each other and from the stigma. Later, but still in early bud, the anthers become firmly connate to each other and adnate to the stigma. The adnation apparently is caused, at least in part, by the many pollen tubes that grow through the anther wall into the stigma, binding these structures

together. More pollen grains per anther are produced by the cleistogamous flowers than by the chasmogamous ones.

Nothing is known of pollination in *Epifagus*. The presence of a nectary (in, curiously enough, both kinds of flowers) suggests insect pollination, but the lack of fruit from most chasmogamous flowers may indicate that the cross-pollination possibly required for fruit development is at best infrequent.

The means of dispersal of *Epifagus* seeds is not known. When the capsule opens, the minute seeds are at first firmly attached by the long funiculi. Even though soon free, they tend to cohere, thus reducing the effectiveness of wind dispersal. The seeds can be dislodged from the capsule by drops of water that fall into its opening, which faces upward and is fully exposed to the impact of raindrops.

When the seeds are shed, the embryo is several celled and undifferentiated, but by the following spring it appears as a "many-celled body enlarged at one end and tapered abruptly into a nearly filamentous structure at the opposite end" (Brooks). According to my field observations (in Indiana and Louisiana), germination takes place usually in spring. By mid-June the plants are smooth, spherical, undifferentiated, whitish "tubercles" 1/16 to 1/4 inch in diameter. Such tubercles apparently can be found in fall (Schrenk), suggesting that beechdrops may behave sometimes as a "winter annual." By July, the tubercles are about 1 inch long. Their tapering upper portion bears numerous imbricate scale-leaves, some of which may subtend flower buds. Short roots arise from the lower portion. Growth from here on is rapid, and by August fairly mature plants may be found. Although *Epifagus* is generally considered to be a fall-flowering (August–November) species, it is not always so. I have collected plants in eastern Texas bearing mature seeds in June. These plants probably developed from seeds that germinated the previous fall. Beechdrops plants, dry and brittle, persist over the winter but the following spring show no sign of life, their tuberous bases being in various stages of decay. There seems little doubt that *Epifagus* is an annual plant.

The vascular system is a dictyostele, consisting of usually bicollateral vascular bundles, with the phloem exceeding the xylem in extent. In the inflorescence the bundles are regularly arranged in a ring, but in the tuber they show "a most confused and irregular arrangement, running in all directions and planes apparently" (Cooke & Schively). However, Brooks noted, in the tuber, that the phloem "follows a very irregular branching pattern" but "the xylem masses . . . are arranged in a ring." The bast fibers are greatly developed in the inflorescence, giving it its stiff and elastic nature. Brooks found no evidence of a cambium in *Epifagus*.

The roots, called "grapplers" by Fergus, have neither root caps nor endodermis. The cortical parenchyma cells closest to their small central vascular bundle have greatly thickened cell walls; it is these cells that account largely for the stiffness and rigidity of the roots.

Cooke & Schively reported that endosperm formation, after fusion of the polar nuclei, begins before fertilization in *E. virginiana* and that the second male gamete is non-functional. This report of "precocious albumen" requires confirmation.

Beechdrops was once of some notoriety as a medicinal herb. Three of its common names — cancer-root, clap-wort, and flux-plant — attest to the variety of its uses.

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2. **Conopholis** Wallroth, Orobanches Generis Diaskeue 78. 1825.

Low, glabrous to glandular-pubescent, cream, yellow-brown, or brown, simple or very rarely branched perennials. Base of plant an enlarged irregular "tuber" ("gall") covered with thick porous bark; secondary roots lacking. Stem densely covered with imbricate leaf-scales below, these becoming scattered and alternate above. Inflorescence racemose, each flower with [1] 2 bractlets [or none], short- to long-pedicelled. Calyx tubular, split anteriorly ("spathaceous"), 2- or 4–5-toothed or -lobed. Corolla tubular, frequently arcuate, persistent for a time on the enlarging capsule, 2-lipped, the upper lip external, erect, rounded, notched or rarely 3- or 4-lobed, the lower lip erect to spreading, 3-lobed or rarely 1- or 2-lobed, the lobes rounded to acute. Stamens exserted; anthers free, anther halves somewhat divergent, mucronulate basally. Style elongate, persistent or deciduous, included or exserted; stigma capitate, slightly depressed centrally to horizontally furrowed. Capsule ovoid to ellipsoid, dehiscing irregularly or anteroposteriorly. Seeds small, numerous, triangular, quadrangular, or rhomboidal; testa smooth, marked with darker lines forming a reticulum. TYPE SPECIES: *C. americana* (L.) Wallr. (*Orobanche americana* L.). (Name from Greek, *conos*, cone, and *pholis*, scale, the appearance of the plant suggesting a pine cone — especially to those who have never seen a pine cone.) — SQUAW ROOT.

A North American genus of two allopatric species. *Conopholis americana*, $2n = 40 \pm 2$, squaw-root, ranges from Nova Scotia to Upper Michigan and Wisconsin south to northern Florida. The similar *C. alpina* Liebm., ranging from Arizona and New Mexico south to Panama, is distinguished from *C. americana* by the greater length-width ratio of its leaf-scales and bracts, by its denser and thicker inflorescence, and by its style being usually deciduous from the fruit. Haynes, the recent monographer of *Conopholis*, recognized two varieties of *C. alpina* — var. *alpina* and var. *mexicana* (Gray ex Watson) Haynes — distinguished by range, texture of leaf-scales, and vestiture. *Conopholis americana* and *C. alpina* are so closely related that they could well be considered conspecific. However, Haynes preferred to treat the eastern and western populations as two species because of their reproductive isolation, their morphological

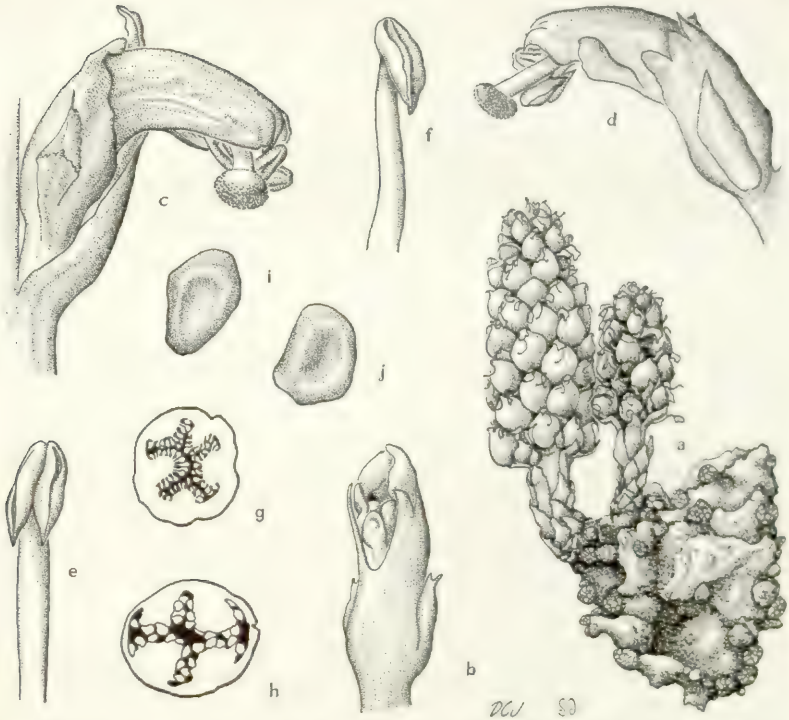

FIGURE 2. **Conopholis.** a–j, *C. americana*: a, fruiting plant detached from root of *Quercus rubra*, which was to right — note scaly buds on "tuber." × 1/2; b, bud, from below to show calyx with two bractlets and aestivation of petals, × 4; c, d, lateral views of two flowers, × 4; e, f, two stamens, × 8; g, diagrammatic cross section of ovary with five placentae, × 6; h, diagrammatic cross section of fruit with four placentae, × 2; i, j, two seeds, × 12.

distinctness, and their apparent host specificity. So far as is known, the two taxa approach no closer than about 800 miles to each other. The oaks available as hosts for the two species differ. Only *Quercus Muehlenbergii* and *Q. virginiana*, neither known to be parasitized by *Conopholis*, occur sympatrically with both species of the genus. Whether one species of *Conopholis* could parasitize the hosts of the other is not known.

While genera other than *Quercus* have been reported to be hosts for *Conopholis*, in all cases where the parasitized root has been traced to its origin, it has been found to belong to an oak. Boeshore and Percival indicated the hosts to be members of the red oak group (*Quercus* subg. ERYTHROBALANUS), but Doak reported that *Q. bicolor*, one of the white oaks (subg. QUERCUS), was parasitized. According to literature and herbarium label data, *C. americana* parasitizes members of both oak groups, including *Q. alba*, *Q. bicolor*, *Q. borealis* (= *Q. rubra*), *Q. falcata*, *Q. hemispherica* (= *Q.* × *laurifolia*), *Q. marilandica*, *Q. nigra*, *Q. petraea* (in the Botanical Garden at Copenhagen; see B. Tiagi, 1965), *Q. rubra*,

Q. Shumardii, and *Q. velutina*. Many of these records require confirmation. Collectors of *Conopholis* should attempt to ascertain — not always an easy task — the host plant. If this cannot be done, at least a piece of the parasitized root should be collected to permit identification, by means of wood anatomy, of the oak group to which the host belongs.

The mature plant of *Conopholis americana* consists of one or more flowering shoots that arise endogenously from an enlarged "gall" attached to an oak root. The root does not usually extend past the "gall." The flowering shoots are annual, but the "gall" is perennial, perhaps living up to several years before flowers are produced. "Galls" are recorded to range from 0.5 to 10 inches in diameter and are irregularly shaped. Large conglomerate masses may be formed by the fusion of two or more (to at least 18) "galls." The "galls" may be completely subterranean or be partially exposed at the soil surface. The "gall" is covered with a thick, porous dark brown bark and is composed of "innumerable granules of sclerenchyma" (Wilson) and parenchyma. The aggregates of stone cells are its most prominent feature.

The nature of the "gall" is uncertain. Wilson regarded it as "in the main, a modification of the host" caused by the "irritant action of the parasite" that brings about "swelling up of the host root, and enormous multiplication of its sclerenchyma patches." Boeshore concurred. Percival, however, interpreted the "gall" as consisting "almost entirely of the stem tissues of the parasite, apparently in more or less disorganized arrangement." He noted that cambial activity is greater — with more secondary tissues — in the base of the shoot than higher and that it is greater yet in the "gall." In the "gall" there is a pronounced increase in the amount of secondary tissue, resulting from "a very active cambium which is sufficient to explain the excessive hypertrophy." The vascular bundles can be traced directly from the shoot through the "gall" to their junction with the xylem of the host root.

Wilson noted stomata on the epidermis of the shoot but none on the leaves. The stomata were apparently vestigial and the guard cells functionless, the stomata being either open or closed (Percival). Boeshore found some misshapen and poorly developed stomata on the outer surface of the upper leaves. The leaves are devoid of palisade tissue.

Little is known concerning pollination in *Conopholis*. Haynes observed a bumblebee visiting a flower of *C. americana* in Georgia. He reported only one additional pollination record, based on herbarium label data, for the genus: bumblebees on *C. alpina* var. *alpina* in Tamaulipas. Evidence that *Conopholis* may, at least occasionally, be self-pollinated in the bud was found by Haynes: a slide of pollen from dehisced anthers from a bud of an alcohol-preserved plant of *C. americana* showed that about one-half of the pollen grains had already germinated.

The seeds of *Conopholis* are large and few relative to those of other Orobanchaceae. Their highly diversified shapes develop as a result of pressure exerted by the enlarging ovules. Double ovules and seeds are frequent. Nothing is known of seed dispersal in the genus.

The early stages in the life history of *Conopholis* are almost unknown. Percival tried various ways to germinate seeds of *C. americana*, both in the field and in the laboratory. His study, which involved about 22,000 seeds, showed negative results except where the seeds were in proximity to oak roots. The embryos of several of these seeds showed "a modification of cell content and absorption of food from the endosperm." These changes may have represented the first stage in germination. A single seed was found to have developed a radicle that had attained a length of 3 mm. before it came into contact with and penetrated an actively growing oak root tip.

The vascular system of the shoot is a dictyostele composed of two (Boeshore, Wilson) or three (Chatin, Percival) rings of bundles. That the inner ring is much less prominent than the others may account for the different interpretations of ring number. Wilson described the bundles as collateral, with the xylem and phloem inverted in the bundles of the inner ring; Boeshore interpreted the bundles as being bicollateral. Percival, whose account probably is the most reliable, regarded the bundles as collateral, with those of the middle ring having inverted xylem and phloem. He identified a cambium in the bundles of the outer and middle rings.

Percival was unable to locate sieve tubes and companion cells in the phloem of *Conopholis americana*, although Wilson had reported the presence of both these cell types. The phloem, according to Percival, is made up of phloem parenchyma — which he regarded as "apparently quite useless as a conductive tissue, the more so since it was often completely crushed in the basal section of the flowering shoot. The xylem vessels were numerous and well developed; they evidently are the main pathways for the conduction of food and water from the host." Percival considered it logical to assume that any *Conopholis* cells could obtain dissolved foods from contiguous cells of the host because of the difference in sap concentration reported by Doak.

An interesting reaction of the host root to *C. americana* is the gradual infiltration of tannin into the root tissues adjacent to the tissues of the parasite. The older a "gall" becomes, the more completely the vascular tissues of the host are infiltrated and plugged until, at length, the "gall" dies and disintegrates, leaving an oak root well protected by tannous deposits against attack by decay-producing organisms.

So far as is known, *Conopholis* is of no economic importance. An extract of the whole plant of *C. americana* is said to possess insecticidal properties.

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3. **Orobanche** Linnaeus, Sp. Pl. **2**: 632. 1753; Gen. Pl. ed. 5. 281. 1754.

Low, glandular-pubescent to nearly glabrous, yellowish to tan, sometimes reddish- or bluish-tinged, simple or branched annuals or perennials. Base of plant slender to enlarged; secondary roots present. Stem covered with imbricate leaf-scales below, these becoming scattered and alternate above. Inflorescence racemose or spicate or rarely of a single flower, each flower ebracteolate [or bibracteolate], sessile to long pedicelled. Calyx campanulate and [4-]5-toothed to [4-]5-parted, or split anteroposteriorly into 2 lateral segments, these entire to 2-lobed. Corolla tubular, more or less arcuate, often marcescent, the lobes subequal to strongly unequal, the limb obscurely to strongly 2-lipped, the upper lip external or internal, notched or 2-lobed, the lower 3-lobed, the lobes rounded. Stamens included; anthers free, anther halves parallel to somewhat divergent, mucronulate basally. Style elongate, usually persistent, included or exserted; stigma variable, commonly crateriform, bilamellate, or 2-lobed. Capsule ovoid to ellipsoid, dehiscing anteroposteriorly, the valves sometimes remaining attached at their tips. Seeds minute, numerous, cylindric, ovoid, or ellipsoid; testa finely reticulate. (Including *Aphyllon* Torr. & Gray in Gray, *Myzorrhiza* Phil., and *Thalesia* Raf.) LECTOTYPE SPECIES: *O. major* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **3**: 234. 1913. (Name from Greek, *orobos*, vetch, and *anchein*, to strangle, in allusion to the plants' parasitic habits. — BROOMRAPE.

The largest genus of Orobanchaceae, with about 100 species, a majority (about 90 species of sects. OROBANCHE and TRIONYCHON) native to Eurasia and Africa, especially the Mediterranean region, about 10 species (sects. EUANOPLON and MYZORRHIZA) American. Several Old World species are widely distributed weeds. Each of the four sections of *Orobanche* has been accorded generic status by various workers; Beck-Mannagetta's inclusive interpretation of the genus is almost universally accepted today. In the southeastern United States, *Orobanche* is represented by one native and one introduced species, which belong to different sections.

Section EUANOPLON (Endl. ex Walp.) Thieret [5] (§ *Aphyllon* (Torr. & Gray) G. Beck and § *Gymnocaulis* Nutt.), with two species, is characterized by its long-pedicelled, ebracteolate flowers and by its campanulate, subregular, 5-cleft to 5-parted calyx. It is represented in the southeastern United States by *O. uniflora* L. var. *uniflora* (*Aphyllon uniflorum* (L.) Torr. & Gray in Gray; *Thalesia uniflora* (L.) Raf.), $2n = 36, 72$ (in a diploid-parthenogenetic form). The species ranges, in several too confluent varieties, over much of extreme southern Canada (including Newfoundland) and the conterminous United States but is not yet recorded from Manitoba, Saskatchewan, South Dakota, Arizona, New Mexico, and Louisiana. Its habitats include moist to dry deciduous or mixed woods, stream banks, rocky glades, and grassy roadsides; it has been recorded as parasitic on *Artemisia*, *Aster*, *Coreopsis*, *Lithophragma*, *Potentilla*, *Quercus*, *Sedum*, *Solidago*, and *Tellima*.

According to Smith, the roots of *Orobanche uniflora* (rarely present on herbarium specimens) are thick and fleshy and branch freely. He distinguished two kinds of roots: those forming parasitic connections, and the "soil roots," which do not. The soil roots seem functionless in absorption, probably serving as supporting organs. Neither kind of root possesses root hairs or root cap. The vascular tissues are disposed in a diarch or, less often, a triarch arrangement. The phloem exceeds the xylem in extent. Sieve tubes seem to be absent.

The vascular system of the stem is a dictyostele composed of a ring of collateral bundles, with the phloem better developed than the xylem. Sieve tubes are lacking; the phloem consists of "elongated elements with granular contents, which are sometimes nucleated." The xylem consists of "tracheae." Smith could not, with assurance, identify a cambium. He concluded further that the xylem has no conductive function but serves solely to support and strengthen the plant.

Achey recognized two species in sect. EUANOPLON, *Orobanche uniflora* and *O. fasciculata* Nutt. Usually rather easily distinguished, the two seem connected by occasional specimens of intermediate morphology. *Orobanche fasciculata* var. *subulata* Goodman, described from Oklahoma, is not easily placed in either species, at least on the basis of herbarium material. A biosystematic study of sect. EUANOPLON is a desideratum.

Section OROBANCHE (§ *Ospreolen* Wallr.), with about 60 species, is the

[5] **Orobanche** sect. **Euanoplon** (Endl. ex Walp.) Thieret, comb. nov. *Anoplanthus* sect. *Euanoplon* Endl. ex Walp., Repertorium 3: 480. 1844.

largest section of the genus. It is characterized by its sessile or nearly sessile, ebracteolate flowers and by its calyx, deeply cleft anteroposteriorly into two lateral segments, each of which is entire to two-lobed. It is represented in southeastern United States by an introduced Mediterranean species, *O. minor* Sm., $2n = 38$, collected from several counties in Florida and North Carolina, where it is recorded as parasitizing *Crotalaria*, *Nicotiana*, *Petunia*, and *Trifolium*. Beck-Mannagetta lists many additional host species. *Orobanche minor* has been alleged to be toxic to cattle and goats.

Some work (Holdsworth & Nutman) indicates that *Orobanche minor* does not initiate flowers unless the host has reached the flowering condition. To what extent other broomrapes follow this pattern is not known, although flowering in "several strains" of *Orobanche* occurs on hosts that are in purely vegetative condition (Kribben).

An additional section, TRIONYCHON Wallr., characterized by its bibracteolate flowers and its mostly 4-lobed calyx, is represented in the United States by the introduced *O. ramosa* L., $2n = 24$, a Eurasian species that has been collected on *Cannabis* in Kentucky and that may yet be found in the Southeast.

The flowers of *Orobanche* are homogamous or, more rarely, proterogynous. They may or may not secrete nectar. Pollination in some species is by insects, especially Hymenoptera. In other species, the flowers appear to be self-pollinated. The seeds are distributed mainly by wind and by rain wash. They have been shown to pass unharmed through the digestive tract of cattle but subsequently to be rendered inviable during fermentation of the feces.

Chromosome counts are available for members of all four sections of *Orobanche*: EUANOPLON, $2n = 36, 72$ (one species); MYZORRHIZA, $2n = 24$ (one species); OROBANCHE, $2n = 38$ (12 species) or 38, 40 (one species); and TRIONYCHON, $2n = 24$ (three species). Gardé suggested that six is the basic number for the genus and that those species having 38 chromosomes are heteroploids, $6n + 2$.

As angiospermous parasites of agricultural plants, various species of *Orobanche* rank in importance with the witchweeds (*Striga* and *Alectra*, of the Scrophulariaceae) and the dodders (*Cuscuta*, of the Convolvulaceae). Various methods are used to control *Orobanche*. Weeding is effective for infestations of limited extent if it is carried out over the several weeks that broomrape shoots may appear. "Catch crops," plants that serve as hosts for the parasite, may be sown and then, before the parasite has produced mature seeds, be plowed under. "Trap crops," plants that do not serve as hosts but do stimulate the germination of *Orobanche* seeds, have been used with some success. Control with chemicals has shown promise, especially certain hormone-type sprays and soil fumigation with methyl bromide. Biological control with phytophagous insects or parasitic fungi has been suggested. The breeding of *Orobanche*-resistant strains of crop plants is under investigation, especially in *Helianthus*.

Successful use of an extract of *Orobanche crenata* to treat kidney stones has been reported (Ibrahim).

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 15. A STUDY OF THE LEAFY HEPATIC FLORA OF THE LUQUILLO MOUNTAINS

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THE LUQUILLO MOUNTAINS, a part of the 28,000 acre Luquillo National Forest, are situated in the northeastern part of the island of Puerto Rico (FIGURE 1). At low elevations the mountain slopes are covered with a luxuriant montane rain forest, while at somewhat higher elevations palm forests are dominant. The summits of some of the mountains are covered by dwarf forests of stunted trees and shrubs and are known as "mossy" or elfin forests. In all three vegetation regions, moderate temperature (20–24°C range during the course of a year), frequent (usually daily rains), and fairly low incident global radiation (Gates, 1969) provide climatic conditions conducive to the development of a luxuriant leafy hepatic flora.

The leafy Hepaticae are abundant and widespread throughout the Luquillo Range, covering the ground, tree trunks, branches, shrubs and leaves at all elevations, but it was not known whether the distribution of all the species was uniformly widespread, or whether elevation, microclimate, and other edaphic factors which vary from place to place were reflected in restricted patterns of distribution. To ascertain whether changes in composition of the hepatic flora do occur with changes in elevation and microclimate, etc., a total of 740 random collections were made in ten fairly distinct areas of the Luquillo Mountains during February of 1967. A permanent slide was made for every species found in each collection, and a list of species present was compiled for each area. Treating each of the collections as a sample quadrat, the frequency of each species was determined for each of the ten areas by dividing the number of collections in which a species was found in an area, by the total number of collections made in that same area (TABLE 1). In addition the ten areas were compared, using Sørensen's (1948) coefficient of community, to assess the degree of floristic similarity among them (TABLE 2). In this method the number of species common to two areas is simply expressed as a percentage of the total number of species of those areas; e.g., 37.2% of the species found in areas 1 and 2 are common to both areas, while the remaining 62.8% of the species are found in only one of

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[2] We wish to thank Dr. Richard Howard for his assistance as our guide to Pico del Oeste and to El Yunque. He has also supplied the lists of flowering plants for the study areas. Both Dr. Carroll Wood and Dr. Howard collected hepatics for us on Pico del Oeste thus giving our survey a more comprehensive coverage for Dr. Howard's study area here.

FIGURE 1. Map of Puerto Rico with an enlargement of the study region in the Luquillo National Forest. The numbers 1 through 10 indicate the ten areas of investigation. (1) low elevation roadside; (2) rain forest around the La Mina Recreational area; (3) Mt. Britton Loop or Route 191; (4) U.S.D.A. La Mina Station; (5) entrance to the El Toro trail; (6) high elevation savanna; (7) summit of Pico del Oeste; (8) summit of Mt. Britton, (9) summit of El Yunque; and (10) summit of El Toro.

the two (TABLE 2). Finally, utilizing the unweighted pair-group method with arithmetic averages of Sokal and Sneath (1963), a cluster analysis was made of the similarity coefficients of the ten areas or communities and a dendrogram based on percent similarity was constructed (FIGURE 2).

DESCRIPTION OF THE TEN STUDY AREAS

Area 1. This area is defined as a region of relatively low elevation (200 meters) approximately 8.0 kilometers north of the La Mina Recreational Area (FIGURE 1). The 28 collections made here were restricted to the more or less disturbed vegetative areas along the highway. Although the rainfall of this region appears to be approximately equal to that found at the La Mina Recreational Area, the microclimate of the hepatic flora is much drier because along the roadside the tree trunks and soil are much more affected by drying breezes and increased solar radiation than they are in the dense, shaded forest. The adventive vegetation in this area consists of shrubs and seedling trees. *Heterotrichum cymosum*, *Lantana camara*, *Eupatorium odoratum*, *Inga vera*, *Cecropia peltata*, *Casearia guianensis*, *Cordia globosa*, *Piper hispidum* with *Rubus rosaefolius* and *Gleichenia bifida* forming tangles. The most often encountered species, in the order of their frequency of occurrence * are: *Lopholejeunea sagraeana* and *Ceratolejeunea maritima*, both of which are widespread on the trunks of large *Cecropia* trees. *Lejeunea flava*, *Cyclolejeunea convexistipa*, *Euosmolejeunea trifaria*, *Harpalejeunea subacuta*, *Alobiellopsis dominicensis*, and *Calypogeia laxa* are also significant elements * of the hepatic flora of this region with the latter two being common on soil and the others, on the trunks of large specimens of *Cecropia*, bamboo, and tree ferns. In this exposed area of roadside plants were found two species, *Archilejeunea viridissima* and *Ptychocoleus polycarpus*, which were not encountered in any of the other nine areas of study.

Area 2. The second area comprises the montane rain forest surrounding the La Mina Recreational Area and Restaurant (FIGURE 1). At an elevation of approximately 400 meters, the average annual rainfall of this area is 300 cm. per year (Recher & Recher, 1966). The rains are frequent and usually heavy with rapid clearing following each torrential shower. The phanerogamic flora appears to be highly diversified, with buttressed trees and lianas forming a dense canopy 40 to 50 feet or more above the forest floor. The large size and spreading branches of the trees allow for a more or less open spacing below the canopy. The principal trees and shrubs are *Dacryodes excelsa*, *Magnolia splendens*, *Guarea ramiflora*, *Xanthoxylum martinicense*, *Nectandra patens*, *Myrcia deflexa*, *Alchornea latifolia*, *Sapium laurocerasus*, *Croton poecilanthus*, *Miconia tetrandra*, and *Ixora ferrea*. A small stream with banks lined with large rocks and boulders, traverses the rain forest just below the restaurant and contrib-

* For percent frequency of occurrence see TABLE 1.

utes to a fairly large waterfall in the northern part of the collecting area.

A total of 86 species of leafy Hepaticae were found in the 116 collections made from the trees, shrubs, vines, leaves, boulders, and soil in this area. The most often encountered species in the order of their frequency of occurrence * were *Macrolejeunea subsimplex*, *Cyclolejeunea convexistipa*, *Trichocolea elliottii*, *Ceratolejeunea maritima*, and *Plagiochila divaricata*. Other significant species * in the hepatic flora include *Prionolejeunea aequitexta*, *Drepanolejeunea fragilis*, *Bazzania schwaneckiana*, *Lophocolea martiana* and *Ceratolejeunea cornuta*. Of particular interest is the fact that here in the rain forest 14 species were found that were not encountered in any of the other nine areas. Listed in the order of their frequency of occurrence * these include *Ceratolejeunea rubiginosa*, *Plagiochila amoena*, *Odontolejeunea lunulata*, *Plagiochila tamariscina*, *Ceratolejeunea cubensis*, *Cheilolejeunea decidua*, *Leptolejeunea elliptica*, *Stictolejeunea squamata*, *Lophocolea guadeloupensis*, *Drepanolejeunea lichenicola*, *Bazzania eggersiana*, *Crossotolejeunea bermudiana*, *C. boryana*, and *Lopholejeunea mülleriana*.

Area 3. The roadside regions of the Mt. Britton Loop road or Route 191 are designated as study area 3 (FIGURE 1). The overall elevation is 750 meters and the rainfall is approximately equal to that of area 2. As in area 1, collecting was restricted to more or less disturbed habitats such as roadside rocks, trees and shrubs, a large pile of decaying palms, a ravine, and the sides of a concrete bridge. The common shrubs found here were *Heterotrichum cymosum*, *Miconia racemosa*, *Mecranium amygdalinum*, *Cyrilla racemiflora*, *Clibadium erosum*, and *Lobelia assurgens*. As expected, these less shaded localities provide a drier microclimate for the hepatic flora than that found within the rain forest proper.

The leafy hepatic flora of this area is fairly well diversified, nonetheless, with 55 species occurring in the 40 collections made. Those most often encountered in the order of their frequency of occurrence * were *Cyclolejeunea convexistipa*, *Ceratolejeunea maritima*, *Taxilejeunea sulphurea*, *Cyclolejeunea chitonia*, *Drepanolejeunea inchoata*, and *Macrolejeunea subsimplex*. In addition, *Herberta divergens*, *Plagiochila rutilans*, *Trichocolea flaccida*, *Diplasiolejeunea pellucida*, and *Drepanolejeunea fragilis* also form a significant part of the flora. Only one of the species found here, *Calypogeia caespitosa*, was not found elsewhere.

Area 4. Here are included the soil banks and small, stunted shrubs and trees surrounding the U.S.D.A. La Mina Station, about 3 kilometers south of the La Mina Recreation Area (FIGURE 1). The area has been disturbed frequently by man. Adventive shrubs are dominated by *Gonzalagunia spicata* and *Eupatorium odoratum*. Herbaceous plants, especially on the exposed banks, consisted of *Sida carpinifolia*, *Polygala paniculata*, *Elephantopus scaber*, *Sauvagesia erecta*, *Synedrella nodiflora*, *Borreria brachysepala*, *Blechnum occidentale*, and *Lycopodium cernuum*. The ele-

* For percent frequency of occurrence see TABLE 1.

vation is only slightly higher and the microclimate more open and exposed to the winds of the mountain pass, so that the area is considerably more xerophytic than Area 3.

Only 32 species of leafy hepatics occurred in the 55 collections made in this area, a fact which might be related to the larger number of hepatics here occurring on the soil bank along the highway. Dominant species in the order of their frequency of occurrence * include *Ceratolejeunea maritima*, *Syzygiella perfoliata*, *Taxilejeunea sulphurea*, *Neurolejeunea breutelii*, *Cyclolejeunea convexistipa*, *Ceratolejeunea patentissima*, and *Leucosarmentum portoricense*. Other species of significance are *Neesioscyphus bicuspidatus*, *Harpalejeunea uncinata*, *Leucolejeunea xanthocarpa*, and *Omphalanthus filiformis*. Only one species, *Microlejeunea monoica* was found only in this area.

Area 5. A total of 92 collections was made in this area, which consisted of rain forest and disturbed roadside vegetation approximately 5.0 kilometers south of the La Mina Recreation Area, 2.0 kilometers south and down the mountain from area 4. (FIGURE 1). In the vicinity of the entrance to the El Toro Trail, this area has an elevation of approximately 700 meters and a microclimate quite similar to that described for area 3. The trees in this area are primarily species of *Nectandra*, with *Cyrilla racemiflora*, *Sapium laurocerasus*, *Alchornea latifolia*, *Croton poecilanthus*, and *Calycogonium squamulosum*. Those of smaller stature included *Miconia pubescens*, *Ditta myricoides*, *Casearia decandra*, and *Hedyosmum arborescens*.

Fifty-one species were collected in the area. The most often encountered species in the order of their frequency of occurrence * were *Ceratolejeunea maritima*, *Cyclolejeunea convexistipa*, *Neurolejeunea breutelii*, *Cyclolejeunea chitonia*, *Lejeunea flava*, *Bazzania gracilis*, and *Plagiochila abrupta*. Within this area were three species, *Symbiezidium laceratum*, *Euosmolejeunea clausa*, and *Lopholejeunea howei* which were not found in the other areas.

Area 6. This area includes a large grassy ridge along the U.S. Navy Road to East Peak near the base of Pico del Oeste. (FIGURE 1). When the road was constructed in 1965, this region was disturbed and since then has been populated with numerous species of tall sedges and grasses and a few scattered trees and shrubs. Although rains are frequent, the open savanna type vegetation allows for rapid drying.

The "grassy" savannas at this altitude present an unusual ecological niche. Scattered or grouped shrubs or small trees are of compact habit. *Clusia grisebachiana*, *Tabebuia rigida*, *Ocotea spathulata*, *Hirtella rugosa*, *Cyrilla racemiflora*, *Byrsonima spicata*, and *Daphnopsis americana* are the most abundant plants. The "grassy" appearance is due to several species of *Rhynchospora* mixed with *Nepsera aquatica*, *Lycopodium cernuum*, and *Pitcairnia angustifolia*. Three species of *Utricularia* have been found and *Lycopodium meridionale* occurs adhering tightly to the wet soils.

* For percent frequency of occurrence see TABLE 1.

The leafy hepatics found in this region occur on leaves, branches, and trunks of the scattered trees, on blades of the grasses and sedges, and on soil. Of the 43 species * found in the 41 collections made here *Ceratolejeunea maritima*, *Taxilejeunea sulphurea*, *Frullania atrata*, *Ceratolejeunea patentissima*, and *Omphalanthus filiformis* were the most widespread. Other species of significance included *Drepanolejeunea fragilis*, *D. inchoata*, *Herberta divergens*, *Plagiochila bursata*, and *Cyclolejeunea convexistipa*. Unlike all of the other areas studied, no species were found which appeared to be restricted to this area alone.

Area 7. This area is the "mossy" or elfin forest on the summit of Pico del Oeste (FIGURE 1). At an elevation of 1020 meters the vegetation of this region is almost constantly exposed to a mean wind speed of 14 mph and is shrouded in clouds and mist for at least 60% of the daylight hours (Baynton, 1968; 1969). The rainfall is approximately 453 cm. per year (Lyford, 1969), the mean annual temperature is 18.6°C (Baynton, 1968), relative humidity ranges from 85% to 99% (Gates, 1969; Baynton, 1969), and the average incident global radiation on the forest floor is 0.8 cal. $cm.^{-2}$ min^{-1} as compared to an incident global radiation of 1.3 cal. $cm.^{-2}$ min^{-1} in San Juan (Gates, 1969).

As Howard (1968) has pointed out, the phanerogamic flora of this region is very different from that found at lower elevations in the Luquillo Mountains. The dense forest is composed of twisted trees from eight to twelve feet in height with *Tabebuia rigida* and *Ocotea spathulata* being the dominant components of the canopy. Herbaceous and woody climbers like *Ipomoea*, *Rajania*, *Hornemannia*, and *Gonocalyx* along with trailing branches of *Marcgravia sintenisii* contribute to a small part of the canopy and make the subcanopy an almost impenetrable thicket.

In all parts of the forest leafy Hepaticae cover the ground, trees, branches, and vines, often forming dense cushions up to a foot thick or hanging in festoons two to three feet in length. In the 95 collections made in this area there were 60 species. As shown in an earlier paper (Fulford, Crandall & Stotler, 1970), the species occurring most often, in the order of their frequency of occurrence * were *Ceratolejeunea valida*, *Cystolejeunea lineata*, *Drepanolejeunea inchoata*, *Bazzania longa*, *Prionolejeunea aemula*, *Plagiochila confundens*, *Herberta divergens*, *Trachylejeunea inflexa*, *Plagiochila bidens*, and *Colura rhynchophora*. Other widespread species * include *Cyclolejeunea accedens*, *Drepanolejeunea fragilis*, *Lepidozia patens*, *Ceratolejeunea patentissima*, *Cyclolejeunea convexistipa*, and *Radula saccatiloba*. Four species were on this peak which were not found on any of the peaks or in the forests at the lower elevations: *Calypogeia elliottii*, *Nowellia dominicensis*, *N. caribbeania* and *Odontoschisma prostratum*.

Area 8. Mt. Britton comprises study area 8 (FIGURE 1). Reaching an elevation of 941 meters, Mt. Britton is the lowest and hence the least exposed

* For percent frequency of occurrence see TABLE 1.

of the mountain peaks studied. According to Recher and Recher (1966) the average annual rainfall on the summit is 500 cm. per year and the average temperature is 22°C. The phanerogamic vegetation of Mt. Britton is best described as a Sierra palm forest (Recher & Recher, 1966) with *Euterpe globosa* comprising 80% of the canopy. Even at the summit the trees, which are mostly palms, are 20 to 40 feet in height and are more or less openly spaced. The peak is generally windswept and often enveloped in clouds, but not to the same extent as Pico del Oeste.

A total of 112 collections were made of the hepatic flora of Mt. Britton; some of the samples were taken from the region around the observation tower on the summit of the mountain, others were from an old road cut somewhat below the summit, and still others were from lower elevations along the Mt. Britton trail above the Loop Road. Among the 88 species found here, the more abundant ones listed in the order of their frequency of occurrence * are *Ceratolejeunea maritima*, *Cyclolejeunea convexistipa*, *Neesioscyphus bicuspidatus*, *Prionolejeunea acmula*, *Plagiochila bursata*, *Cystolejeunea lineata*, *Bazzania stolonifera*, *B. hookeri*, *Odontoschisma longiflorum*, *Trichocolea flaccida*, *Bazzania gracilis*, and *Trichocolea elliottii*. Four species, *Symbiezidium transversale*, *Bazzania bidens*, *B. cubensis*, and *Marchesinia brachiata* were found only in this area.

Area 9. This area comprises the forest at the summit of El Yunque (FIGURE 1). With an elevation just 50 feet higher than Pico del Oeste the microclimate and vegetation of this area are very similar to those of Pico del Oeste. According to Brisco (1966), the mean wind speed on El Yunque is 13 mph, the mean relative humidity is 98%, and the incident global radiation at noon ranges from 0.3 cal. cm^{-2} min^{-1} to 0.8 cal. cm^{-2} min^{-1}. The peak is covered by clouds, mist, and rains most of the time.

The vegetation of this peak, as described by Gleason and Cook (1927), is that of the mossy or elfin forest with four species constituting 75% of the canopy: *Weinmannia pinnata*, *Ocotea spathulata*, *Eugenia borinquensis*, and *Tabebuia rigida*. Although the overall appearance of the stunted, twisted trees and dense undergrowth is similar to that described for Pico del Oeste, there are some differences in the two areas, as for example, the presence of *Podocarpus coriaceus* on El Yunque (Dansereau, 1966) and its absence on Pico del Oeste (Howard, 1968).

While most of the 85 samples made in this area were taken along the foot trail through the forest itself, some were also made on El Yunque Rock, an exposed granite outcrop almost devoid of vegetation. Sixty-eight species of leafy hepatics were found in the El Yunque area. The more abundant of these listed in the order of their frequency of occurrence * are *Cystolejeunea lineata*, *Lepidozia patens*, *Plagiochila chinantlana*, *Ceratolejeunea valida*, *Plagiochila bursata*, *Syzygiella perfoliata*, *Cyclolejeunea convexistipa*, *Herberta divergens*, and *Bazzania longa*. Only

* For percent frequency of occurrence see TABLE 1.

one species, *Herberta elliottii*, was found here and not in any of the other nine study areas.

Area 10. El Toro, the tenth study area, is not only the highest peak in the Luquillo Range with an elevation of 1074 meters, but is also the farthest inland of the peaks studied (FIGURE 1). Because of its higher elevation and its geographical location, the summit of El Toro is much more xerophytic than the other peaks. Rains are less frequent, and the peak is free of clouds for at least 90% of the daylight hours. The winds, which blow constantly, and a fairly high solar radiation have a pronounced drying effect on the exposed portion of the peak.

At the summit itself, the vegetation is more like that of a montane scrub than of an elfin forest (Dansereau, 1966). Sarmentose trees and shrubs, among the large rocks and exposed outcroppings devoid of soil, reach a height of only three to eight feet, and the forest lacks the lianas and vascular epiphytes so common to El Yunque and Pico del Oeste. *Mitropsidium sintenisii*, *Miconia foveolata*, *Toralbasia cuneifolia*, *Eugenia borinquensis*, and *Ilex sintenisii* occur along with the more common *Cyrilla racemiflora*, *Tabebuia rigida*, *Ocotea spathulata*, *Symplocos micrantha*, and *Haenianthus salicifolius*.

In a few more protected areas below the summit a more typical moist elfin forest occurs. The general aspect of this latter forest resembles that of the summits of El Yunque and Pico del Oeste. At still lower elevations this more or less stunted forest grades into a palm forest, whereas on the summit of Mt. Britton, the Sierra palm (*Euterpe globosa*) forms a dominant part of the canopy. Finally, at an elevation of approximately 775 meters, the palm forest opens into a dry, grassy ridge that runs between El Toro and one of the neighboring peaks. In this latter region grasses and sedges are widespread and the windswept trees and bushes range from three to fifteen feet in height.

All four of these vegetation types, montane scrub, elfin forest, palm forest, and grassy ridge, were sampled in the 78 collections made on El Toro. Of the 91 species found, the more abundant, listed in the order of their frequency of occurrence * are *Omphalanthus filiformis*, *Ceratolejeunea patentissima*, *C. flagelliformis*, *Cyclolejeunea convexistipa*, *Ceratolejeunea maritima*, *Plagiochila bursata*, *Ceratolejeunea valida*, *Cystolejeunea lineata*, *Drepanolejeunea inchoata*, *Frullania atrata*, *Syzygiella perfoliata*, and *Prionolejeunea aemula*. Surprisingly, only one species, *Calypogeia lophocoleoides*, was not found in other areas.

DISCUSSION

In the ten areas treated in this study a total of 156 species of leafy hepatics were encountered. Only five of these species, *Ceratolejeunea maritima*, *C. patentissima*, *Cyclolejeunea convexistipa*, *Drepanolejeunea fragilis*, and *Frullania subtilissima* were present in all ten study areas

* For percent frequency of occurrence see TABLE 1.

(TABLE 1). *Drepanolejeunea inchoata* and *Taxilejeunea sulphurea* were found in nine of the ten areas, while *Calypogeia peruviana*, *Neesioscyphus bicuspidatus*, *Ceratolejeunea valida*, *Harpalejeunea heterodonta*, *Macrolejeunea subsimplex*, *Neurolejeunea breutelii*, and *Prionolejeunea aemula* were present in eight. Only these fourteen species, however, appear to be dispersed generally throughout the Luquillo bryoflora, apparently without regard to elevation or microclimate.

The remaining 142 species have various more restricted distribution patterns. For example, roughly 18% of the species were found only in the rain forest and roadsides of the lower elevations, areas 1 through 6, and not at all in the palm, elfin, or montane forests of the four mountain peaks. These species and their areas of distribution are as follows: [3]

1. *Archilejeunea viridissima* — 1
2. *Bazzania eggersiana* — 2
3. *Bazzania schwaneckiana* — 1 and 2
4. *Calypogeia caespitosa* — 3
5. *Ceratolejeunea brevinervis* — 3, 5, and 6
6. *Ceratolejeunea cubensis* — 2
7. *Ceratolejeunea rubiginosa* — 2
8. *Cheilolejeunea decidua* — 2
9. *Crossotolejeunea bermudiana* — 2
10. *Crossotolejeunea boryana* — 2
11. *Drepanolejeunea lichenicola* — 2
12. *Euosmolejeunea clausa* — 5
13. *Frullania exilis* — 3 and 4
14. *Leucosarmentum portoricense* — 4, 5, and 6
15. *Leptolejeunea elliptica* — 2
16. *Lophocolea guadeloupensis* — 2
17. *Lopholejeunea howei* — 5
18. *Lopholejeunea mülleriana* — 2
19. *Microlejeunea monoica* — 4
20. *Odontolejeunea lunulata* — 2
21. *Plagiochila amoena* — 2
22. *Plagiochila bicornis* — 2 and 6
23. *Plagiochila distinctifolia* — 2, 4, and 5
24. *Plagiochila tamariscina* — 2
25. *Ptychocoleus polycarpus* — 1
26. *Stictolejeunea squamata* — 2
27. *Symbiezidium laceratum* — 4

16% of the species were encountered only in the forests on one or more of the mountain peaks and not at all in the rain forest below. In this group are included the following: [3]

1. *Bazzania bidens* — 8
2. *Bazzania cubensis* — 8
3. *Bazzania stolonifera* — 7, 8, 9, and 10
4. *Calypogeia cellulosa* — 7, 9, and 10
5. *Calypogeia elliottii* — 7

[3] Numbers following each name indicate the areas of distribution of each species.

6. *Calypogeia lophocoleoides* — 10
7. *Cephalozia subforficata* — 8 and 10
8. *Diplasiolejeunea unidentata* — 7, 8, and 9
9. *Herberta elliotii* — 9
10. *Jungermannia dominicensis* — 8 and 9
11. *Lepidozia patens* — 7, 9, and 10
12. *Leptoscyphus gibbosus* — 7 and 9
13. *Marchesinia brachiata* — 8
14. *Micropterygium carinatum* — 7, 8, 9, and 10
15. *Nowellia dominicensis* — 7
16. *Nowellia caribbeania* — 7
17. *Odontoschisma prostratum* — 7
18. *Plagiochila chinantlana* — 7, 8, 9, and 10
19. *Plagiochila dominicensis* — 7 and 10
20. *Plagiochila simplex* — 8, 9, and 10
21. *Prionolejeunea exauriculata* — 7 and 10
22. *Radula fendleri* — 7, 8, and 9
23. *Symbiezidium transversale* — 8
24. *Syzygiella rubricaulis* — 7, 9, and 10
25. *Trachylejeunea inflexa* — 7 and 10

Finally, still other species (approximately 20% of the flora) were restricted to only one of the ten study areas as noted previously in the descriptions.

The flora of each of the study areas then, is composed both of widespread elements which are more or less characteristic of the entire Luquillo bryoflora, and of more specific elements which do reflect the elevation, microclimate, and possibly even the geographical isolation of the area itself. Community comparisons using Sørensen's (1948) coefficient of community indicate that all of the areas have a similarity coefficient of at least 25.3%, while many areas have much higher percentages of similarity (TABLE 2). In most cases there is less similarity between the low elevation areas and the mountain peaks than there is among the peaks or low elevation areas themselves.

Area 1 (low elevation roadside) has fairly low similarity coefficients with all of the other areas, suggesting that it has a more or less distinct flora, while area 2 (rain forest at the La Mina Recreational Area) appears to be most similar to the forests of area 8 (Mt. Britton) and area 10 (El Toro). Areas 3, 4, 5, and 6, all more or less recently disturbed habitats of higher elevation than area 1, appear to possess numerous common species with similarity coefficients of 45.3% to 55.2%. Area 3 (Mt. Britton Loop) also has over 50% of its species in common with area 8 (Mt. Britton), area 9 (El Yunque), and area 10 (El Toro). Areas 5 (entrance to El Toro trail) and 6 (high elevation savanna) bear over 50% of their species in common with areas 8 (Mt. Britton) and 10 (El Toro). Within the mountain peaks themselves, Pico del Oeste (area 7) is most like El Yunque (area 9) with a similarity coefficient of 67.7%, while Mt. Britton (area 8) most closely resembles El Toro (area 10) with a similarity coefficient of 69.3%.

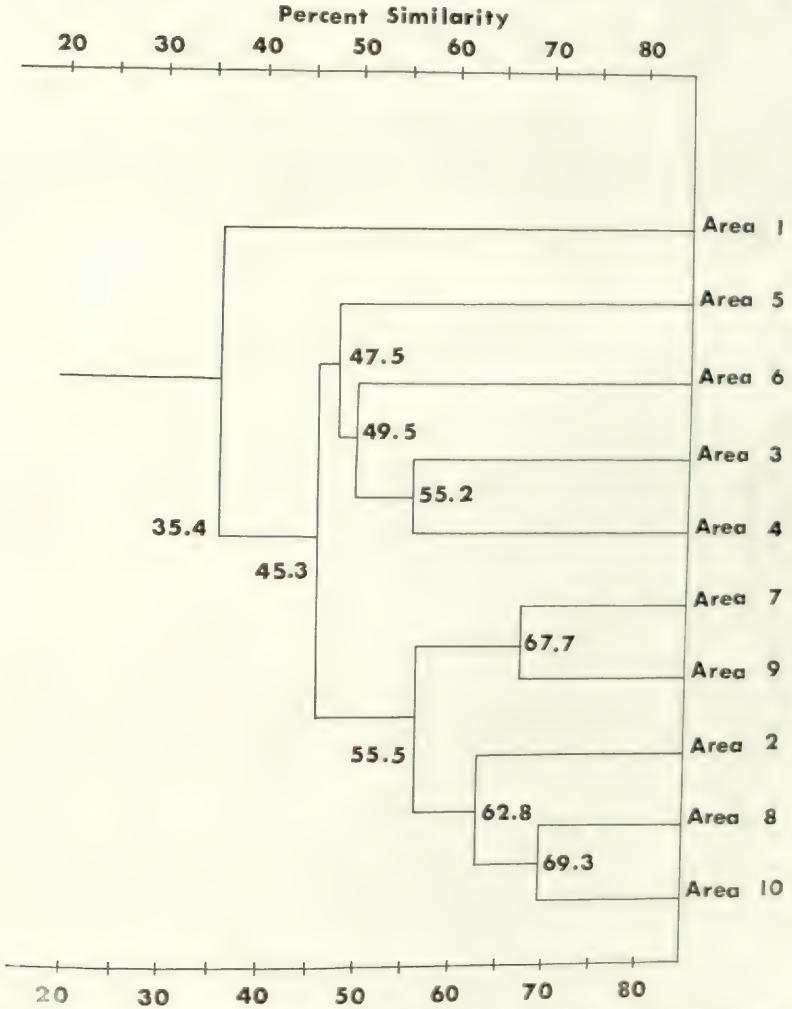

FIGURE 2. Dendrogram of the hepatic floras of ten study areas of the Luquillo Mountains, obtained by the unweighted pair group method with arithmetic averages of Sokal and Sneath (1963). Area 1 refers to a low elevation roadside; area 2, to the rain forest around the La Mina Recreational Area; area 3, to the Mt. Britton Loop; area 4, to the U.S.D.A. La Mina station; area 5, to the entrance region to El Toro; area 6, to a high elevation savanna; area 7, to Pico del Oeste; area 8, to Mt. Britton; area 9, to El Yunque; and area 10, to El Toro.

The dendrogram prepared from a cluster analysis of the similarity coefficients substantiates the relationships shown by the coefficients of community (FIGURE 2). Again area 1 is seen to have a more or less distinct flora as it does not group with any of the other nine areas. Areas 3, 4, 5, and 6 form one cluster group with area 3 (Mt. Britton Loop) being

TABLE 1. **Frequency of Occurrence of Leafy Hepaticae in Ten Study Areas of the Luquillo Mountains**

AREA NUMBER	1	2	3	4	5	6	7	8	9	10
TRICHOCOLEACEAE										
Trichocolea										
brevifissa Steph.		1.7%	2.5%	1.8%				2.7%		1.3%
elliottii Steph.		19.8%	2.5%	1.8%				10.7%	1.2%	1.3%
filicaulis Steph.		3.5%						1.8%	2.4%	
flaccida (Spr.) Jack & Steph.		6.9%	10.0%				2.1%	11.6%	3.5%	11.5%
scraps		2.6%								
ISOTACHIDACEAE										
Neesioscyphus										
bicuspidatus (Steph.) Grolle		6.9%		7.3%	1.1%	2.4%	1.1%	21.4%	2.4%	2.6%
HERBERTACEAE										
Herberta										
divergens (Steph.) Herz.			10.0%			12.2%	22.1%	1.8%	17.7%	6.4%
elliottii Spr.									3.5%	
juniperoidea (Sw.) Grolle			5.0%	3.6%				0.9%		3.9%
pensilis (T. Tayl.) Spr.					1.1%		7.4%		8.2%	2.6%
LEPIDOZIACEAE										
Bazzania										
bidens (Nees) Trevis.								0.9%		
breuteliana (Lindenb. & Gott.) Trevis.		4.3%					1.1%	0.9%		

cubensis (Gott.) Pagán							0.9%		
eggersiana (Steph.) Pagán		0.9%							
gracilis (Hampe & Gott.) Steph.		4.3%	2.5%	6.5%			10.7%	5.9%	2.6%
hookeri (Lindenb.) Trevis.		3.5%	5.0%				11.6%	2.4%	2.6%
longa (Nees) Trevis.			2.5%			28.4%	0.9%	15.3%	6.4%
longistipula (Lindenb.) Trevis.		0.9%	2.5%			14.7%		7.1%	6.4%
roraimensis (Steph.) Fulf.			2.5%		2.4%	5.3%	0.9%		7.7%
schwaneckiana (Hampe & Gott.) Trevis.	3.6%	12.1%							
stolonifera (Sw.) Trevis.						1.1%	12.5%	3.5%	9.0%
scraps			1.1%			11.8%		2.4%	2.6%
Lepidozia									
patens Lindenb.						16.8%		30.6%	6.4%
Microlepidozia									
capillaris (Sw.) Fulf.		5.2%		1.1%			5.4%	1.2%	6.4%
Micropterygium									
carinatum (Grev.) Reim.						5.3%	2.7%	12.9%	3.9%
exalatum Steph.			2.5%						
Telaranea									
sejuncta (Ångstr.) S. Arnell		6.9%	2.5%			1.1%	8.0%	1.2%	9.0%
CALYPOGEIACEAE									
Calypogeia									
caespitosa (Spr.) Steph.			2.5%						
cellulosa (Spreng.) Steph.						11.6%		4.7%	2.6%
crenulata Bischl.		0.9%					0.9%	3.5%	
cyclostipa (Spr.) Steph.		1.7%					1.8%		
elliottii Steph.						3.2%			

TABLE 1. **Frequency of Occurrence of Leafy Hepaticae in Ten Study Areas of the Luquillo Mountains** (*continued*)

AREA NUMBER	1	2	3	4	5	6	7	8	9	10
laxa Gott. & Lindenb.	10.7%	3.5%			3.3%			3.6%		2.6%
lophocoleoides Steph.										1.3%
peruviana Nees & Mont.	3.6%	9.5%	2.5%		1.1%		1.1%	9.8%	3.5%	5.1%
CEPHALOZIACEAE										
Cephalozia										
caribbeania Fulf.		1.7%					1.1%	2.7%	2.4%	2.6%
crassifolia (Lindenb. & Gott.) Fulf.		2.6%						0.9%	1.2%	3.9%
subforficata Herz.								1.8%		2.6%
Nowellia										
caribbeania Fulf.							1.1%			
dominicensis Steph.							2.1%			
ODONTOSCHISMACEAE										
Alobiellopsis										
dominicensis (Spr.) Fulf.	10.7%	0.9%	2.5%			2.4%	1.1%	0.9%		1.3%
Odontoschisma										
denudatum (Nees) Dum.					3.3%				1.2%	
longiflorum (T. Tayl.) Steph.		3.5%			4.4%			11.6%		2.6%
prostratum (Sw.) Trevis.							1.1%			
REGREDICAULACEAE										
Arachniopsis										
coactilis Spr.		0.9%						0.9%		

ZOOPSIDACEAE										
Zoopsis antillana Steph.				1.1%			2.7%			
ALOBIELLACEAE										
Alobiella husnoti (Gott.) Schiffn.				4.3%			4.5%	3.5%		
PARACROMASTIGACEAE										
Leucosarmentum portoricense Fulf.			9.1%	3.3%	2.4%					
LOPHOCOLEACEAE										
Heteroscyphus elliottii (Steph.) Pagán	0.9%					1.1%	0.9%		1.3%	
Leptoscyphus gibbosus (T. Tayl.) Mitt.						4.2%		2.4%		
Lophocolea guadeloupensis Steph.	1.7%									
martiana Nees	12.1%	2.5%		4.4%			0.9%		1.3%	
LOPHOZIACEAE										
Syzygiella perfoliata (Sw.) Spr.		7.5%	32.7%	2.2%	9.8%	5.3%		18.8%	15.4%	
rubricaulis (Nees) Steph.						1.1%		7.1%	1.3%	
JUNGERMANNIACEAE										
Jungermannia dominicensis Spr.							0.9%	2.4%		

TABLE 1. Frequency of Occurrence of Leafy Hepaticae in Ten Study Areas of the Luquillo Mountains (*continued*)

AREA NUMBER	1	2	3	4	5	6	7	8	9	10
ADELANTHACEAE										
Adelanthus										
decipiens (Hook.) Mitt.	3.6%						3.7%	0.9%	4.7%	7.7%
PLAGIOCHILACEAE										
Plagiochila										
abrupta Lehm. & Lindenb.		3.5%	7.5%		6.5%	4.9%		1.8%	1.2%	1.3%
adiantoides (Sw.) Dum.			2.5%						4.7%	
amoena Steph.		5.2%								
arcuata Lindenb.	3.6%	5.2%				4.9%		2.7%		2.6%
bicornis Hampe & Gott.		1.7%				2.4%				
bidens Gott.			7.5%				21.1%	1.8%	2.4%	5.1%
breutelioides Lindenb.		0.9%	2.5%					1.8%		
burtiae (Desv.) Lindenb.		0.9%	2.5%			12.2%	6.3%	13.4%	18.8%	21.8%
chiwantiana Gott.							23.3%	4.5%	21.2%	9.0%
confundens Lindenb. & Gott.		3.5			2.2%			0.9%		
distinctifolia Lindenb.		3.5%		3.6%	3.3%					
divaricata Lindenb.		17.2%	5.0%					6.3%		7.7%
dominicensis T. Tayl.							6.3%			2.6%
jamaicensis Lindenb. & Hampe						2.4%	5.3%	6.3%	8.2%	1.3%
nitidula Lindenb.			10.0%	1.8%	2.2%	4.9%	1.1%		2.4%	1.3%
simplex (Sw.) Dum.								8.0%	3.5%	9.0%
subbidentata T. Tayl.		5.2%			1.1%		4.2%	5.4%	2.4%	3.9%
tamarisrina Steph.		3.5%								
?temis Lindenb.		0.9%			1.1%			2.7%		
Scraps	7.2%	9.5%	2.2%	1.8%	2.5%		3.2%	8.0%		2.6%

SCAPANIACEAE										
Scapania										
portoricensis Hampe & Gott.					1.1%		3.2%		1.2%	2.6%
RADULACEAE										
Radula										
fendleri Gott.							5.3%	3.6%	14.1%	
inflexa Gott. ex Steph.			2.5%							1.3%
kegelii Gott. ex Steph.		7.8%						0.9%		
longifolia Steph.		6.0%	7.5%	1.8%	4.4%			1.8%		7.7%
saccatiloba Steph.						2.4%	15.8%	0.9%	2.4%	
spp.		4.3%	5.6%		2.5%			7.1%	1.2%	
FRULLANIACEAE										
Frullania										
atrata (Sw.) Dum.						19.5%				15.4%
brasiliensis Raddi						4.9%			7.1%	1.3%
exilis T. Tayl.			2.5%	3.6%						
kunzei Lehm. & Lindenb.				1.8%						1.3%
subtilissima (Nees & Mont.) Lindenb.	7.1%	1.7%	7.5%	3.6%	1.1%	7.3%	6.3%	0.9%	8.2%	10.3%
LEJEUNEACEAE										
Anoplolejeunea										
conferta (Meissn.) Evans			2.5%							3.9%
Archilejeunea										
viridissima (Lindenb.) Steph.	3.6%									

TABLE 1. Frequency of Occurrence of Leafy Hepaticae in Ten Study Areas of the Luquillo Mountains (*continued*)

AREA NUMBER	1	2	3	4	5	6	7	8	9	10
Ceratolejeunea										
brevinervis (Spr.) Evans			2.5%		1.1%	7.3%				
cornuta (Lindenb.) Steph.		12.1%			1.1%			1.8%		
cubensis (Mont.) Schiffn.		3.5%								
flagelliformis (Steph.) Fulf.				3.6%	4.4%		6.3%	2.7%	7.1%	32.1%
maritima (Spr.) Steph.	17.9%	18.1%	27.5%	40.0%	22.8%	51.2%	9.5%	27.7%	7.1%	26.9%
patentissima (Hampe & Gott.) Evans	3.6%	0.9%	7.5%	10.9%	2.2%	17.1%	16.8%	2.7%	12.9%	38.5%
rubiginosa Steph.		6.0%								
spinosa (Gott.) Steph.		5.2%			4.4%			1.8%		1.3%
valida Evans		0.9%	5.0%		1.1%	7.3%	47.4%	3.6%	21.2%	21.8%
scraps		1.7%	5.6%		2.5%	2.4%	4.2%	6.3%		2.6%
Cheilolejeunea										
decidua Spr.		3.5%								
polyantha Evans					2.2%					1.3%
Colura										
clavigera (Gott. ex Schiffn.) Jovet-Ast			5.0%			2.4%	1.1%			
rhynchophora Jovet-Ast		6.0%				7.3%	19.0%	0.9%	3.5%	5.1%
Crossotolejeunea										
bermudiana Evans		0.9%								
boryana (Mont.) Steph.		0.9%								
Cyclolejeunea										
accedens (Gott.) Evans		2.6%					17.9%		2.4%	2.6%

angulistipa (Steph.) Evans		1.7%						3.6%	4.7%	7.7%
chitonia (T. Tayl.) Evans	3.6%	7.8%	15.0%	3.6%	10.9%	7.3%		4.5%		
convexistipa (Lehm. & Lindenb.) Evans	10.7%	34.4%	30.0%	12.7%	18.5%	12.2%	16.9%	23.2%	18.8%	32.1%
Cyrtolejeunea										
holostipa (Spr.) Evans			2.5%					0.9%	1.2%	
Cystolejeunea										
lineata (Lehm. & Lindenb.) Evans		1.7%				7.3%	43.2%	13.4%	41.2%	21.8%
Diplasiolejeunea										
brachyclada Evans		6.0%	2.5%							2.6%
pellucida (Meissn.) Schiffn.		7.8%	10.0%			2.4%			1.2%	1.3%
unidentata (Lehm & Lindenb.) Schiffn.							11.6%	1.8%	5.9%	5.1%
Drepanolejeunea										
anoplantha (Spr.) Steph.		1.7%		5.5%		4.9%	14.7%	1.8%	1.2%	5.1%
crucianella (T. Tayl.) Evans						2.4%	1.1%			2.6%
evansii Bischl.		0.9%					1.1%			3.9%
fragilis Bischl.	7.1%	12.9%	10.0%	1.8%	2.2%	14.6%	17.9%	1.8%	7.1%	3.9%
inchoata (Meissn.) Schiffn.		3.5%	12.5%	5.5%	2.2%	14.6%	30.5%	7.1%	9.4%	19.2%
lichenicola (Spr.) Steph.		1.7%								
scraps		3.5%								3.9%
Euosmolejeunea										
clausa (Nees & Mont.) Evans					2.2%					
rigidula (Nees & Mont.) Steph.	7.1%	2.6%	5.0%	1.8%				0.9%	1.2%	
trifaria (Nees) Schiffn.	10.7%	0.9%	2.5%							5.1%

TABLE 1. **Frequency of Occurrence of Leafy Hepaticae in Ten Study Areas of the Luquillo Mountains** (*continued*)

AREA NUMBER	1	2	3	4	5	6	7	8	9	10
Harpalejeunea										
heterodonta Evans		0.9%	5.0%	3.6%	1.1%		12.6%	0.9%	4.7%	12.8%
subacuta Evans	10.7%				3.3%	2.4%		0.9%	3.5%	1.3%
uncinata Steph.	3.6%			7.3%		2.4%	13.7%	0.9%	9.4%	12.8%
Hygrolejeunea										
sp.						2.4%			2.4%	
Lejeunea										
flava (Sw.) Nees	14.3%	2.6%	2.5%	3.6%	10.9%	9.8%		4.5%		
Leptolejeunea										
elliptica (Lehm. & Lindenb.) Schiffn.		3.5%								
hamulata Schiffn.		1.7%						0.9%		3.9%
Leucolejeunea										
xanthocarpa (Lehm. & Lindenb.) Evans		0.9%	2.5%	7.3%		2.4%			2.4%	3.9%
Lopholejeunea										
howei Evans					1.1%					
mülleriana (Gott.) Schiffn.		0.9%								
sagraeana (Mont.) Schiffn.	21.4%	6.9%			1.1%			0.9%		
Macrolejeunea										
subsimplex (Nees & Mont.) Schiffn.		3.6%	34.5%	12.5%	3.6%	5.4%		7.1%	2.4%	6.4%

Marchesinia										
brachiata Schiffn.								0.9%		
Microlejeunea										
acutifolia Steph.		1.7%						0.9%		1.3%
bullata (T. Tayl.) Steph.		3.5%	2.5%		2.2%	2.4%				1.3%
laetevirens (Nees & Mont.) Evans	3.6%	5.2%			1.1%			1.8%		
monoica Bischl.				1.8%						
Neurolejeunea										
breutelii (Gott.) Evans	7.1%	4.3%	7.5%	16.4%	13.0%	7.3%	1.1%			1.3%
Odontolejeunea										
lunulata (Web.) Schiffn.		5.2%								
Omphalanthus										
filiformis (Sw.) Nees			5.0%	7.3%	1.1%	17.1%		7.2%	8.2%	39.7%
Prionolejeunea										
aemula (Gott.) Evans		9.5%	5.0%		2.2%	2.4%	24.2%	14.3%	11.8%	15.4%
aequitexta Evans	3.6%	12.9%	2.5%	1.8%				7.1%		2.6%
exauriculata Evans							1.1%			3.9%
helleri Evans		0.9%			2.2%			2.7%		2.7%
innovata Evans		0.9%					3.2%			
scraps		1.7%	6.7%	3.6%	7.5%		5.3%	7.1%	2.4%	9.0%
Ptychocoleus										
polycarpus (Nees) Trevis.	3.6%									
Pycnolejeunea										
schwaneckii (Steph.) Schiffn.					1.1%	4.9%		0.9%		3.9%
Rectolejeunea										
berteroana (Gott.) Evans		3.5%				2.4%		0.9%		1.3%

TABLE 1. **Frequency of Occurrence of Leafy Hepaticae in Ten Study Areas of the Luquillo Mountains** (*continued*)

AREA NUMBER	1	2	3	4	5	6	7	8	9	10
phyllobola (Nees & Mont.) Evans			2.5%	5.5%			1.1%	1.8%		6.4%
Stictolejeunea squamata (Willd.) Steph.		2.6%								
Strepsilejeunea involuta Steph.		6.9%	5.0%	1.8%	2.2%	4.9%	4.2%	17.9%	7.1%	5.1%
Symbiezidium barbiflorum (Lindenb. & Gott.) Evans	7.1%	3.5%	2.5%							2.6%
laceratum Evans					4.4%					
transversale (Sw.) Trevis.								1.8%		
Taxilejeunea obtusangulata (Spr.) Evans	3.6%	1.7%			3.3%	2.4%		0.9%		
sulphurea (Lehm. & Lindenb.) Steph.	7.1%		17.5%	20.0%	3.3%	22.0%	4.2%	5.4%	8.2%	14.1%
Trachylejeunea inflexa Steph.							22.1%			1.3%

most similar to area 4 (U.S.D.A. La Mina Station), and area 5 (entrance to El Toro trail) most closely resembling area 6 (high elevation savanna). The four mountain peaks (areas 7 through 10) and the La Mina Recreational Area rain forest (area 2) form a second cluster group. In this method of analysis, the hepatic flora of the rain forest (area 2) groups with those of Mt. Britton (area 8) and El Toro (area 10), and the flora of Pico del Oeste (area 7) groups with that of El Yunque (area 9). The two most closely related hepatic floras again are those of Mt. Britton (area 8) and El Toro (area 10) with a percent similarity of 69.3%.

From this study it would seem that the composition of the hepatic flora of the Luquillo Range is highly dependent on the microclimate, and to a lesser extent, on the elevation and geographical isolation of the region in question. The similarities of the microclimate in the rain forest proper (area 2) and the palm forests of Mt. Britton (area 8) and El Toro (area 10) might indeed explain why the hepatic flora of area 2 is more like those of areas 8 and 10 than those of its neighboring areas, i.e., areas 3, 4, 5, and 6. It may be that the hepatic flora of Pico del Oeste is most like that of El Yunque because the microclimate of Pico del Oeste is more like that found on El Yunque than that found on either Mt. Britton or El Toro. The fact that area 6 (high elevation savanna) has 52.2% of its species in common with El Toro (area 10) may be related to the fact that some of the collections made in area 10 were made along a dry grassy ridge very much like the savanna of area 6, and the close relationship between the floras of Mt. Britton and El Toro may well have its basis in the similar palm forests found on both.

Characteristics of the microhabitat alone, however, cannot explain completely the differences which occur in the hepatic flora in different parts of the Luquillo Range. Certainly, the restriction of species to one or a few specialized regions must be related to the dispersal mechanisms of

TABLE 2. **Coefficients of Community for Leafy Hepatic Floras in Ten Study Areas of the Luquillo Mountains** *

AREA NO.	1	2	3	4	5	6	7	8	9	10
1										
2	37.2									
3	39.0	51.1								
4	44.1	33.9	55.2							
5	41.0	48.2	45.3	48.2						
6	40.0	38.8	51.0	48.0	48.9					
7	25.3	37.0	43.5	34.8	34.2	48.5				
8	36.5	66.7	51.7	38.3	53.2	44.3	51.4			
9	25.3	44.2	52.0	38.0	43.7	48.6	67.7	64.1		
10	30.5	58.8	61.6	40.7	41.9	52.2	67.5	69.3	67.9	

* The coefficients represent percent species similarity and were calculated following Sørensen's (1948) method.

the plants as well as to differences in elevation and climate. Just how much the composition of the hepatic flora is dependent on dispersal and how much it is dependent on climatic conditions remains problematical.

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MORPHOLOGICAL STUDIES IN CORDYLINE (AGAVACEAE) I. INTRODUCTION AND GENERAL MORPHOLOGY

P. B. Tomlinson and J. B. Fisher

This paper presents the results of an investigation into the habit and vegetative morphology of the genus *Cordyline* which was undertaken as a preliminary to anatomical, developmental, and experimental studies. Later papers will restrict the enquiry to *Cordyline terminalis*, which is typical for the whole genus in most respects but is a particularly useful species for experiment. These studies will be a further contribution to the investigation of tree-like monocotyledons, particularly those within the Agavaceae which have secondary growth (Tomlinson & Zimmermann, 1969; Zimmermann & Tomlinson, 1969; 1970). The first of these papers summarized much of the extensive earlier literature on these plants. Information specific to *Cordyline* is quite limited, however, and in particular the post-seedling phase of development in this genus (even though it was illustrated as early as 1852 by Gaudichaud-Beaupré), has never been described fully. In making good this deficiency we will show how an understanding of this phase of individual development is necessary in explaining the growth habit of *Cordyline* in possible evolutionary terms.

TAXONOMY

Earlier botanical literature does not distinguish clearly between *Cordyline* and the closely related *Dracaena*, which is understandable in view of their similar habit. Many species of the former genus were described within the latter. However, more recently accumulated information reveals that *Cordyline* is distinct from *Dracaena* in several exomorphic features of which fruit structure is the most constant and readily demonstrated (Brown, 1914).

The two genera are also clearly circumscribed in their vegetative anatomy as was shown in considerable detail by Rothert (1909). Further investigations continue to support these distinctions. Secondary vascular tissues are present in the stems of both genera, but only in *Dracaena* does it also develop in the roots. *Cordyline* has a distinct "rhizome" morphology, described below, for which there is no equivalent in *Dracaena*. Leaf anatomy in *Dracaena* is distinctive because of the unusual arrangement of vascular bundles, as has been confirmed more recently by Wunderlich (1950). Major differences between the two genera are summarized in Table I.

The close relationship between the two genera is otherwise accepted by most authors, whereas their place within the larger classification of monocotyledons remains uncertain. Whether they should remain within the Liliaceae (e.g. Krausse, 1930), or be segregated as members of a

TABLE I. Major diagnostic differences between Cordyline and Dracaena

CORDYLINE	DRACAENA
Ovules many (2 or more) per loculus	Ovules one per loculus
Fruits with several small seeds	Fruits with 1–3 large seeds
Germination epigeous (e.g. *C. australis*) or hypogeous (e.g. *C. terminalis*)	Germination hypogeous
Post-seedling stage rhizomatous	Post-seedling stage not rhizomatous
Roots without secondary tissue	Roots able to develop secondary tissue
Primary vascular bundles of stem amphivasal	Primary vascular bundles of stem collateral
Vascular bundles of leaf normally* orientated (xylem adaxial)	Some vascular bundles of leaf always horizontally orientated* (xylem and phloem perpendicular to normal orientation)
Crystal cells (other than raphides) present	Crystal cells (other than raphides) absent
Ultimate inflorescence unit a solitary flower	Ultimate inflorescence unit often a cincinnate cluster
Bracteole† bifid (often apparently two)	Bracteole† not bifid (evidently single)

* We verified this difference by comparing leaves of *Cordyline* with leaves from several species of *Dracaena* cultivated at Fairchild Tropical Garden.

† Brown (1914) expressed this difference as "2 bracteoles" in *Cordyline*, versus "1 bracteole" in *Dracaena*. In fact, our examination of young stages of flower development in *C. australis* shows that the bracteole originates as a single encircling structure which becomes 2-lobed by subsequent growth of the flower it encloses (*see* p. 475). This suggests that bracteole morphology is not fundamentally different in the two genera.

separate family, as in the Agavaceae of Hutchinson (1959) is part of a much larger problem which does not concern us at this point and will only be resolved when the whole complex is better understood.

Within *Cordyline* itself, continued anatomical and morphological study suggests that it is a very natural genus, but there is still much uncertainty about the total number of species it contains. *Cordyline*, as presently understood, includes about 12 species (more according to Brown, 1914). New Zealand is one center of distribution with five species which seem to be distinct and which have been relatively well studied. There is one

species, *C. dracaenoides* in South America and two more in eastern Australia. In New Guinea existing collections do no more than hint at poorly understood forms. Other species are described from Norfolk Island, Mauritius, the Mascarenes, and New Caledonia. These in part form the genus *Cohnia*. Hybrids between natural populations of distinct species in New Zealand have been described (Cockayne & Allan, 1934).

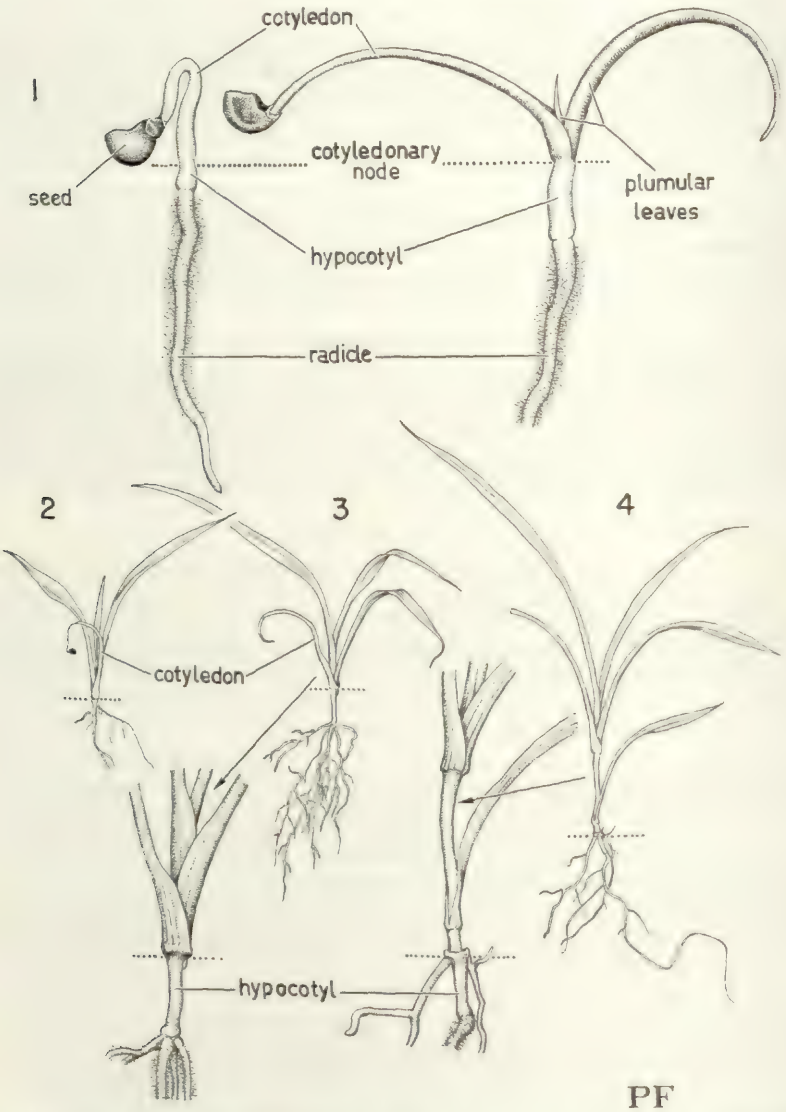
One species which offers particular difficulties is the familiarly cultivated *Cordyline terminalis* which seems to have a wide natural distribution in the Polynesian area, a range which has been so much extended by use of the plant for food, fiber, medicine, and as an ornamental that its original home has become obscure. Many cultivars are known and this has lead to nomenclatural problems where the more striking varieties have been given specific names. The solution to all these taxonomic complexities lies outside the scope of this present work, although it should be mentioned that there are important diagnostic features of leaf anatomy which may be of ultimate value in clarifying the situation (Tomlinson, unpublished). None of these problems is discussed further because we are dealing only with a limited number of the more clearly circumscribed forms. The background of morphological information we provide should, however, prove helpful in the future taxonomic revision which is still necessary.

MATERIAL AND METHODS

Only a minority of species has been investigated, but in view of the naturalness of *Cordyline* it is reasonable to assume that observations are applicable to the genus as a whole. The most extensive investigations were carried out on natural populations of the four commonest [1] species native to New Zealand (*Cordyline australis*, *C. banksii*, *C. indivisa*, and *C. pumilio*) together with varieties of *C. stricta*, an Australian species cultivated in Auckland. Additional material both of wild and cultivated specimens from Fiji and New Guinea, referable to *C. terminalis* has been examined. More extensive observations were also made on old specimens representing several cultivars of *C. terminalis* grown in the Miami area. Early stages of seedling development of *C. australis* and *C. banksii* were observed in plants grown in pots in a greenhouse from seeds collected in the wild. Studies of post-seedling stages have been made on plants of a wide range of sizes dug up in the wild. For studies of seedling morphology in *C. terminalis*, seeds from cultivated plants were sown and large stocks of seedlings were raised. Localities and sources of material are listed in the Appendix. Plants for continuing anatomical and morphological study have been preserved either in formalin-acetic-alcohol or 4 percent formalin. Habit drawings in the figures were all made from either fresh or fluid-

[1] The fifth species, *C. kaspar*, is very rare since it is endemic to the Three Kings Islands just off the northern tip of the North Island of New Zealand. These islands were discovered and named by Abel Tasman on the eve of Twelfth Night, 1643 (Oliver, 1956). Presumably the particular specific name *kaspar* was considered more euphonious than *melchior* or *balthazar*!

preserved specimens. Photographs were used to produce the habit diagrams of mature specimens shown in FIGURES 12 to 18.



FIGURES 1–4. **Cordyline australis.** Seedling: 1, early stages in germination; left, seed at soil level, cotyledon extended but recurved; right, later stage with plumular leaves visible and cotyledon erect, all × 3; 2, stage with cotyledon shrivelled apically, seed coat still attached, × 1/2; 3, later stage, cotyledon unshrivelled, seed coat detached, × 1/2, enlargement, below left, × 1 1/2, shows seedling internodes unextended; 4, similar stage but showing seedling with extended internodes (detail below left), × 1/2.

SEEDLINGS

The genus *Cordyline* is unusual amongst monocotyledons because germination may be either epigeous or hypogeous, depending on the species. For each species the type of germination seems constant. Epigeous germination has been observed in *C. australis* and *C. banksii*; hypogeous germination in *C. terminalis*.

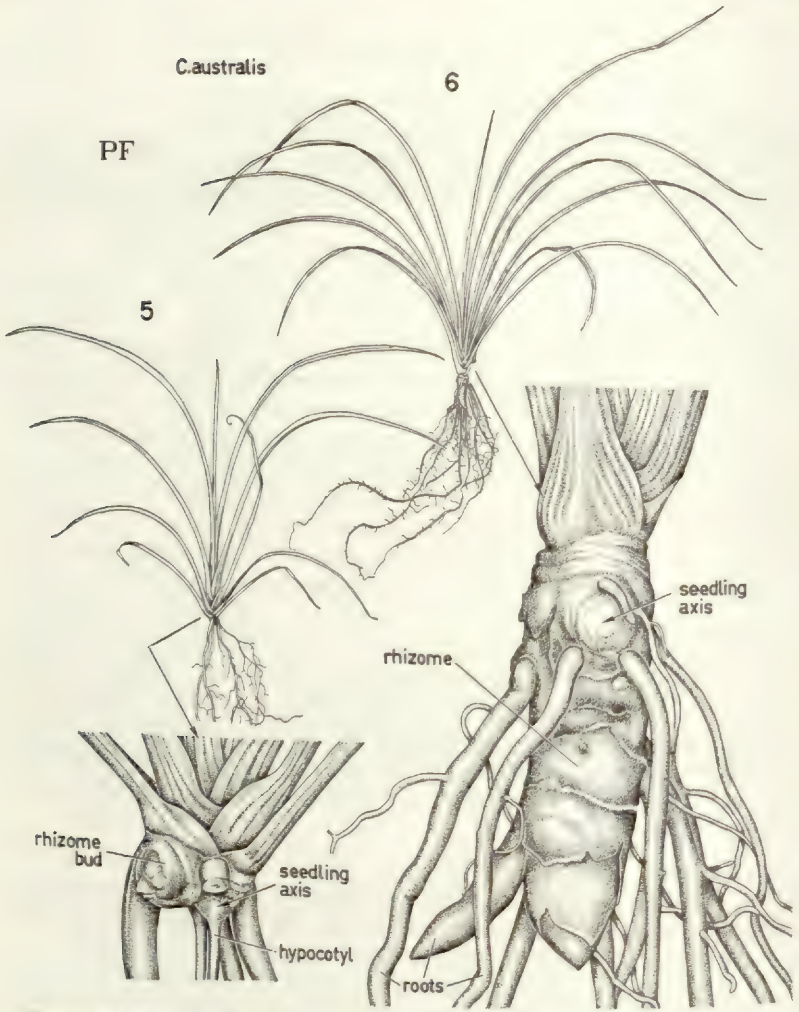
Epigeous. Germination of seeds and early stages of seedling growth were studied in *Cordyline australis* and *C. banksii*. The two species seem identical in all respects (FIGURES 1 to 6). Germination is epigeous, the slender cotyledon becomes erect and green, usually carrying the seed with it (FIGURES 1, 2). Extension of the radicle precedes that of the cotyledon. The hypocotyl is always elongated up to a length of 5 mm., and since it remains glabrous it is clearly delimited from the radicle which has a dense covering of short hairs. The cotyledonary node becomes somewhat swollen and marks the distinct upper limit of the hypocotyl (FIGURES 2, 3). The first adventitious root normally may appear either at this node (FIGURE 4) or at the base of the hypocotyl (FIGURE 3). The plumular leaves are initially enclosed by the base of the cotyledon but later grow through the mouth of the cotyledonary sheath (FIGURE 1). Internodes between early leaves may remain short (FIGURE 3) but are successively wider in the manner characteristic of monocotyledons in their "establishment" phase of growth (Tomlinson & Zimmermann, 1966). Frequently, however, one or more internodes above the hypocotyl becomes extended in varying degrees as is shown in FIGURE 4. This produces a long seedling axis and may be a mechanism for adjusting the depth in the soil at which the plant becomes established.

Hypogeous. *Cordyline terminalis* is distinctive in that germination is hypogeous, the greater part of the cotyledon remaining within the seed and both remaining beneath the soil surface. Details will be presented in the second paper of this series since it deals solely with this species.

All seedlings are alike in subsequent stages of growth. Adventitious roots in seedlings with extended internodes may or may not be restricted to nodes. This restriction is not obvious in later stages because internodes are congested.

POST-SEEDLING DEVELOPMENT

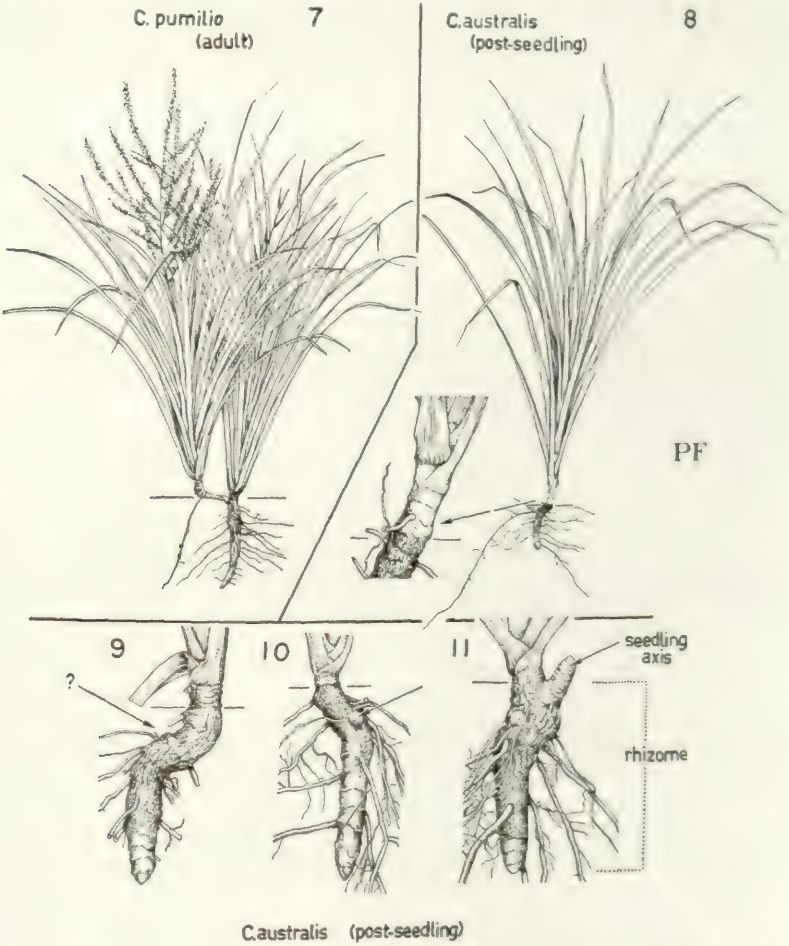
General morphology. Further development continues for a longer or shorter period, in a way normal for large woody monocotyledons. Leaves are successively larger (longer and wider) and the axis widens progressively by establishment growth. The resulting axis is bluntly obconical (FIGURE 5, seedling axis). Leaves each subtend a bud although these buds remain strongly inhibited. There is then an abrupt change in growth pattern, in a way which represents a marked departure from normal monocotyledonous



FIGURES 5 and 6. **Cordyline australis.** Origin of seedling rhizome: 5, habit of seedling, × 1/4, enlargement of axis showing rhizome bud originating from seedling axis, × 3; 6, habit of seedling, × 1/6, enlargement of base of axis to show well-developed rhizome (the parental seedling axis almost obliterated), × 3.

seedling growth. One of these axillary buds develops as a shoot with rapid growth, at first obliquely outward and then vertically downward (FIGURES 5, 6). This shoot produces only fleshy scale-leaves, never foliage leaves. We will refer to this organ as the seedling rhizome. It was illustrated by Arber (1925, p. 50) who called it a "stolon." This distinction is one of definition only, and it is part of the larger problem involved in describing the underground parts of monocotyledons (cf. Tomlinson, 1970; p. 224).

Subsequent growth of the seedling rhizome is so rapid that the existing axis is displaced laterally. It may persist as a more or less distinct appendage. The age and thus the size of the seedling on which the rhizome is initiated varies appreciably and this may account for the variation in size of this appendage itself. FIGURES 9 to 11 show the base of three different



FIGURES 7–11. **Cordyline pumilio** and **C. australis:** 7, *C. pumilio*, adult specimen with two leafy crowns (one flowering) from a single rhizome, × 1/12; 8, *C. australis*, post-seedling specimen comparable to the adult *C. pumilio*, × 1/12, enlargement of axis showing abrupt transition between corky rhizome and smooth aërial stem, × 1/2. 9–11, *C. australis*, details of post-seedling rhizomes with original seedling axes of differing size. all × 1 2: 9, seedling axis obscure, possible site indicated by question mark; 10, seedling axis distinct but small; 11, seedling axis conspicuous, inverted. It is possible to interpret this as the original sapling axis which has died and has been replaced by a lateral shoot.

saplings of *Cordyline australis* of approximately equal size, the right-hand one (FIGURE 11, but see legend) with a conspicuous inverted seedling axis, the left-hand one with the original axis only tentatively identified by the question mark (FIGURE 9) and the middle one recognizable but small (arrow, FIGURE 10). In subsequent growth the sapling retains a single axis without obvious indication that the lower part is a branch of the upper part (FIGURE 8). Both axes grow in diameter at about the same rate. Branching of the seedling axis by development of more than one rhizome bud is possible but the only examples we have seen have been in *C. terminalis*. Branching of the underground parts in later stages of growth seems to involve branching of the rhizome itself. This seems more common in some species (e.g. *C. pumilio*, *C. terminalis*) than in others (*C. australis*, *C. banksii*).

Growth in length of the rhizome at first much exceeds that of the aërial stem. Elongation of the aërial stem does not begin until the axis has reached a diameter of 1 to 2 cm. when the rhizome may be 15 cm. long. Subsequently this aërial axis is the dominant part. Rapid growth of the rhizome in early stages of sapling development is indicated by its smooth white surface and obvious fleshy scale leaves (FIGURE 6) but later the surface becomes wrinkled because cork develops to within a few millimeters of the scaly apical portion (FIGURES 9–11). We have no information about the maximum length to which a rhizome may grow, but in saplings with 2 to 3 m. of visible trunk the rhizome is scarcely longer than in a well-established seedling with the leaf rosette still at soil level.

Rhizome and aërial stem continue their overall diameter growth at roughly similar rates, although the rhizome is usually appreciably wider than the base of the aërial stem, a distinction which persists even in older trees. With the development of a rough bark throughout the whole axis, the original boundary between aërial stem and rhizome becomes lost although it is initially quite sharp (e.g. FIGURE 8). Continued growth of the aërial axis is rapid and since it involves secondary tissues, it leads to the development of a sapling with an unbranched, cylindrical axis which can be several meters long. Branching normally begins with flowering, as is described later. The uniformly cylindrical stem with its secondary tissues obscures the fact that establishment growth of the crown is long continued. The internal features which demonstrate this are described below (p. 468).

In summary, the post-seedling axis of *Cordyline* is unusual, if not unique for angiosperms, in that it has a shoot apex at upper and lower extremity, growing in opposite directions. Functionally, the downward-growing (rhizome) part of the axis serves the same purpose as a tap root, common in dicotyledons but otherwise not developed in monocotyledons.

Lateral primordia of shoot and root occur on the axis. They are suppressed or developed according to circumstances. Buds originate singly in the axils of both foliage and scale leaves and persist indefinitely although they are strongly inhibited. Since they are primary in origin their trace system connects to the primary vascular system in the same way as has

been described for *Dracaena* (Zimmermann & Tomlinson, 1970). Suppressed buds develop into sprouts on stumps of damaged or felled trees. Later papers will indicate how growth of buds is determined and expressed in *Cordyline terminalis*.

Roots of uniform diameter develop on the underground parts (FIGURE 6). Root primordia are also produced in larger numbers over the whole surface of the trunk but they do not normally grow out. They are adventitious, so that their vascular traces are initiated at the surface of the secondary wood. Root traces terminate internally at varying depths within the secondary wood indicating that they are initiated within the cambium over an extended period.

Insofar as they have been examined, other species of *Cordyline* seem to be similar to *C. australis*, *C. banksii*, and *C. terminalis*. *Cordyline indivisa* is an exception because early stages of seedling growth lack the characteristic rhizome which may only appear very late in sapling development. This observation needs verification.

Phyllotaxis. As is usual throughout the monocotyledons leaf arrangement in the seedling is distichous, but there is a rapid change to a spirodistichy in which the angular divergence between successive leaves is somewhat less (or more) than 180°. By the time the seedling rhizome is well established the original distichy is obscured by the pronounced helix of the two "orthostichies." Subsequent development may take either one of two possible courses depending on the species. In the first group of species a true spiral is established, with divergences of the order of 3/8 or higher, as in *Cordyline australis*, *C. indivisa*, and *C. kaspar*. Otherwise, in the second group, the spirodistichy persists as a feature of the adult plant as in *C. banksii*, *C. pumilio*, *C. stricta*, and *C. terminalis*. In these species leaf arrangement may be described as a persistent juvenile feature, in much the same way as distichy in other woody monocotyledons can persist beyond the seedling phase, notably in Strelitziaceae, but also in a few palms. This feature is obvious in such plants, because the distichy is precise, whereas in *Cordyline* it requires close examination to show that there are two ranks of leaves. Spirodistichy is otherwise seen as a juvenile feature in palm seedlings. It should be emphasized that the change from spirodistichy, with two "orthostichies" to a phyllotaxis with several orthostichies involves a major change, namely the addition of entirely new orthostichies to the system of leaves. *Cordyline* thus offers interesting material for the investigation of changing phyllotactic patterns along single shoots in monocotyledons.

Initiation of secondary tissues. Since *Cordyline* develops secondary tissues it is of some interest to know at what stage of development the seedling axis initiates secondary tissue and what relation this bears to rhizome initiation. Secondary tissues can be recognized in transverse section by their uniformly amphivasal bundles without protoxylem, the radial arrangement of ground tissue, and the immature bundles next to a meristematic cambial zone (Cheadle, 1937; Tomlinson & Zimmermann,

1967; 1969). Using these criteria, secondary tissues are evident in the pre-rhizome seedling axis of both *C. australis* and *C. banksii*, at least in the upper (younger) internodes. The central region of primary tissue is complex since it is the result of establishment growth of the type described for the palm *Rhapis excelsa* (Tomlinson & Zimmermann, 1966). The vascular system is further complicated by the attachment of traces from adventitious roots which connect to both primary and secondary bundles. These preliminary observations, however, do show that secondary vascular tissues are initiated prior to the development of the rhizome.

Establishment growth of the seedling of *Cordyline* evidently follows the pattern described in some detail for *Dracaena* (Zimmermann & Tomlinson, 1970), the total number of vascular bundles in the axis being augmented both by the expansion of the crown as well as by secondary tissues. We have made no detailed studies of the course of vascular bundles in seedling axes of *Cordyline* but the close developmental similarity between it and *Dracaena* is not in doubt. As with *Dracaena*, it is evident that establishment growth of the primary cylinder, the result of continued widening of the crown, continues in *Cordyline* for a very long time, well beyond the seedling stage. Measurements for representative young adult specimens of *C. australis* and *C. banksii* are given in TABLE II. These measurements confirm principles which were established by Schoute (1903).

The secondary tissues of mature rhizomes are much less lignified than those of aërial stems; the diffuse secondary vascular bundles are separated from each other by thin-walled, unlignified parenchyma. Primary and secondary tissues are also less clearly circumscribed, one reason for this is that secondary tissues develop early and can be recognized within 5 mm. of the rhizome apex. There is also no sharp boundary either between primary and secondary tissues at the level of attachment of rhizome to parent seedling axis or between the tissues of the two axes. From the anatomical and morphological evidence it seems that the attachment of the developing rhizome to the seedling axis, once it is initiated, is via secondary vascular tissue. In this sense establishment (but not necessarily initiation) of a rhizome bud is dependent on the development of secondary tissue. What is clear from this brief analysis of the seedling axis is that it is a suitable experimental subject.

HABIT

Since early stages are similar in all species it is clear that the general habit of each species is established in the further development of the axis beyond the post-seedling stage. Habit is determined by the overall height which a plant may attain and the frequency of branching, and is indicated diagrammatically in FIGURES 12 to 18 for adult specimens of certain species. Branches are always lateral and from buds in the axils of leaves. These buds are strongly inhibited in naturally grown trees so that saplings are characteristically tall and unbranched. Buds are inconspicuous since

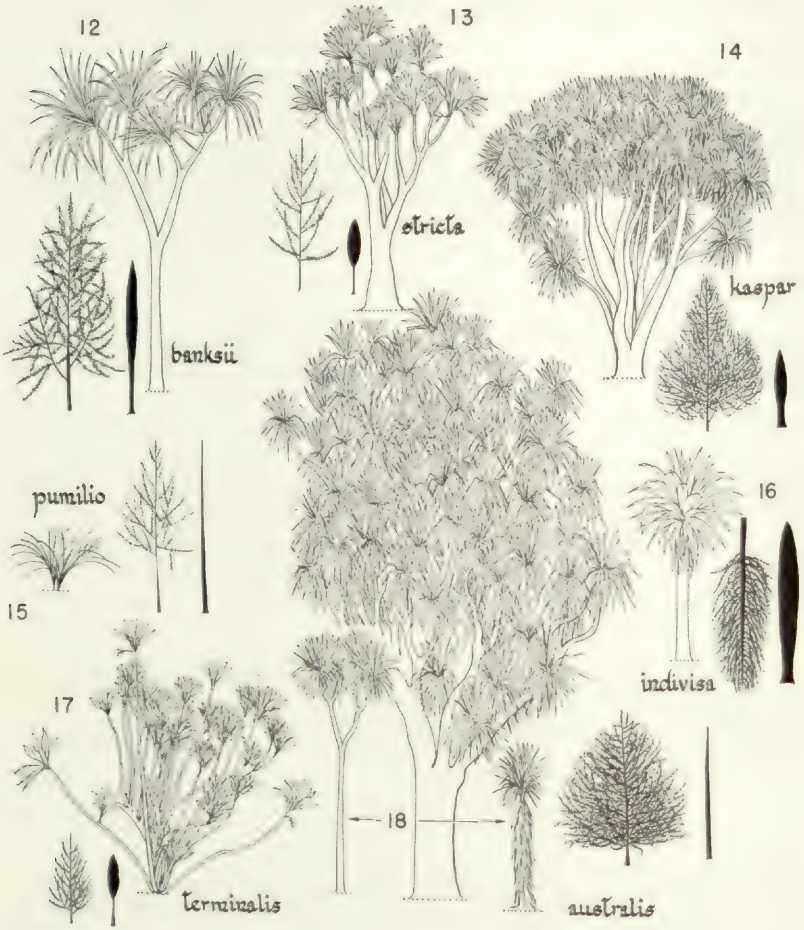
TABLE II. Distribution of primary and secondary tissues in saplings of Cordyline*

LEVEL ABOVE SOIL SURFACE	DIAMETER PRIMARY VASCULAR CYLINDER	AVERAGE WIDTH OF SECONDARY TISSUE†	TOTAL STEM DIAMETER
	A. CORDYLINE AUSTRALIS		
0	2	62.5	137.5
5	7	42.5	112.5
75	10	37.5	95
175	13	32.5	88
255	18	27.5	82.5
290	22	21.5	75
390	27	14.0	66
620	31	7.5	56
	B. CORDYLINE BANKSII		
0	8	61	140
0.5	12	49	120
17	19	43	115
33	23.5	31	95
54.5	27	25.5	87.5
83	29.5	22	83
113.5	31.5	19	80
145.5	34	14	72.5
176	37.5	14	75

* Measurements in mm.
† Average width of cortex is 5 mm.

they consist of a prophyll enclosing a few primordia, the whole organ embedded in the surface tissues of the parent stem, but continuous with the primary vascular cylinder via a few traces which remain largely at a procambial stage of differentiation. Branching is usually the result of flowering although branching in the absence of flowering is not uncommon. When the axis produces a terminal inflorescence a lateral bud close beneath the inflorescence grows out and replaces the previous terminal bud (FIGURE 26). This method of sympodial growth is normal for many woody monocotyledons (Schoute, 1903; Tomlinson & Zimmermann, 1969; Tomlinson *et al.*, 1970). So long as only one bud grows out, the sympodium remains simple. This is the usual condition in *Cordyline indivisa*, whence its name (FIGURE 16), although in a strict morphological sense, the name *indivisa* is misapplied, since the axis, in fact, branches each time it flowers. Mature specimens of this species do occasionally produce divided trunks with more than one crown.

In other species more than one bud may grow out beneath an inflorescence so that the axis as a whole may bifurcate. Three or even four branches are less common beneath a single inflorescence. Forked axes are not dichotomous although there are some misleading reports which suggest this (for a discussion see Tomlinson *et al.*, 1970).



FIGURES 12–18. **Cordyline** species: habit sketches of aërial parts, not to scale. Each illustration includes a sketch of the general appearance of the plant, drawn from photographs, an outline of the leaf, and a silhouette of the inflorescence, drawn either from herbarium specimens or photographs. 12. *C. banksii*; 13. *C. stricta*; 14. *C. kaspar*; 15. *C. pumilio*; 16. *C. indivisa*; 17. *C. terminalis*; 18. *C. australis*, with illustrations of two successive sapling stages to right and left.

Different species fork with different frequency. *Cordyline australis* (FIGURE 18) and *C. kaspar* (FIGURE 14) branch relatively frequently and produce a rather dense crown. The saplings are comparatively little-branched (inset figures in FIGURE 18). *Cordyline banksii* branches sparingly and even at maturity has a slender, little-branched crown (FIGURE 12). This may be related to the shaded forest habitat it occupies.

Species also differ in their tendency to branch from the base. *Cordyline*

australis and *banksii* normally retain a single trunk and are tree-like. *Cordyline terminalis* is more of a shrub since it branches frequently from the base, the aërial shoots in old specimens becoming quite diffuse (FIGURE 17). *Cordyline stricta* is somewhat intermediate between these two extremes and may or may not retain a single trunk (FIGURE 13). The illustration of *C. kaspar* (FIGURE 14) is of a cultivated specimen, the only mature one we have seen.

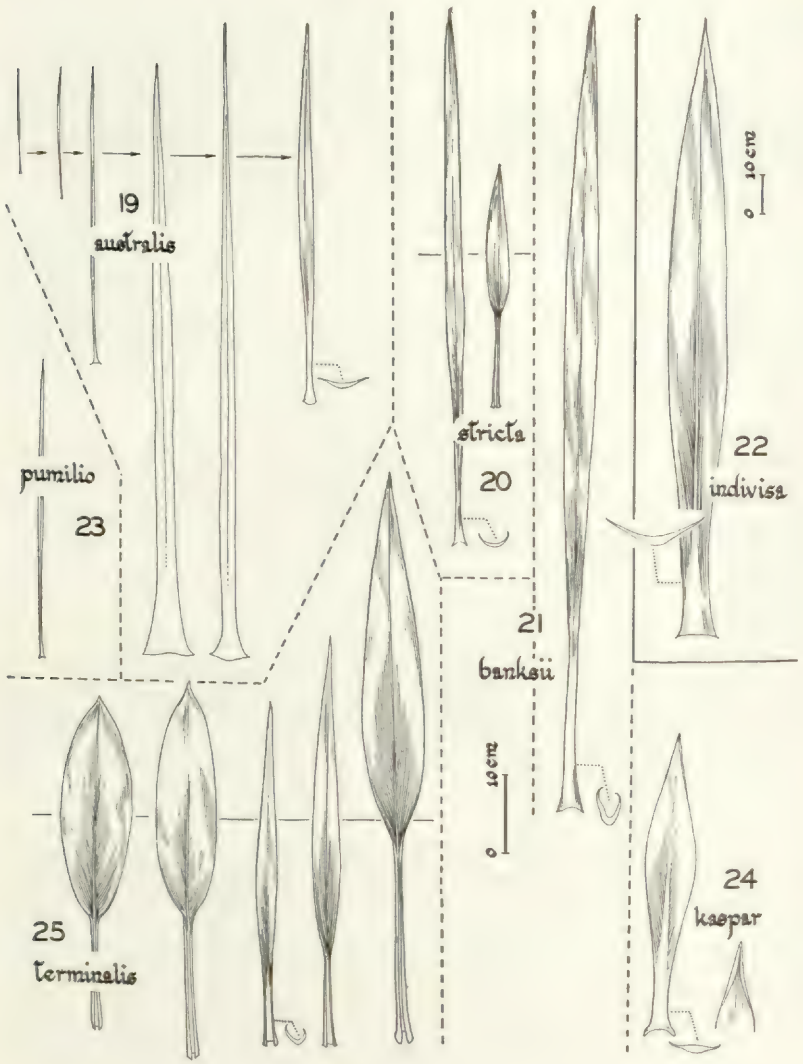
The ability of older plants to branch from the base reflects a tendency for basal buds to develop. This is possible because branching may occur in the absence of flowering, buds being released from inhibition because they are remote from an inhibiting shoot. This type of branching can also occur in distal parts and produces forking stems which resemble sympodial branches. However, monopodial forks can be distinguished in their anatomy from sympodial forks because primary vascular tissues of branch and parent axis are not obviously continuous in the former, whereas they are in the latter (Tomlinson *et al.*, 1970).

Cordyline pumilio is a low-growing herb (FIGURE 15) with one or more rosettes of linear leaves, each rosette supported by a short stem. Underground parts of *C. pumilio* include one or more descending rhizomes which branch readily to produce both new rhizomes and new erect shoots, accounting for the clustered habit of older specimens. In this habit it is seemingly anomalous, compared with the shrubs or trees which otherwise characterize the genus. The anomaly can be explained if *C. pumilio* is equated with the post-seedling stage of development of other, larger species (cf. FIGURES 7 and 8). This suggests that *C. pumilio* is a neotenous form, flowering in the post-seedling stage of development which then persists by branching and without ever forming a tall trunk. It is interesting to speculate to which other species *C. pumilio* is most closely related. The fact that leaves of *C. pumilio* correspond more closely in their anatomy to leaves of seedlings of *C. australis* of approximately the same size (as in FIGURES 19 and 23) than to seedling leaves of any other species may be suggestive. The hypothesis that *C. pumilio* represents a neotenous form of *C. australis* could be tested by further observation and experiment designed to make *C. australis* flower precociously, or to prevent *C. pumilio* from flowering.

The above account describes habit in *Cordyline* in only a very general way. In a subsequent paper we will describe the development of the shoot of *C. terminalis* in more detail with especial reference to the distribution of leafy and rhizomatous shoots.

LEAF MORPHOLOGY

Foliage leaves in seedlings of all species tend to be morphologically alike, but diverge with age in different species. Leaves of *Cordyline indivisa* show the most extreme divergence from the seedling type. A series of leaves representing the change from seedling to sapling and finally to adult is shown for *C. australis* in FIGURE 19. The close resemblance be-



FIGURES 19–25. **Cordyline** species: representative leaves from adult plants, drawn from herbarium specimens; transverse sections of leaves, taken at the level indicated, are shown for all but *C. pumilio*. Note that the leaf of *C. indivisa* is shown at twice the reduction, × 1/18, of all the other figures, × 1/9. 19, *C. australis*, representative leaves from different stages of development of an individual, seedling to the left, sapling in the center, adult to the right; 20, *C. stricta*, adult leaves from two different varieties, to the right with a petiole, to the left lacking one; 21, *C. banksii*; 22, *C. indivisa*; 23, *C. pumilio* (cf. seedling leaves of *C. australis* in FIGURE 19); 24, *C. kaspar*; 25, *C. terminalis*, adult leaves, each representing a different cultivar, from New Guinea populations.

tween the adult leaves of *C. pumilio* (FIGURE 23) and the seedling leaf of *C. australis* is obvious. Adult leaves of other species studied, representing quite fully the range throughout the genus as a whole, are shown in FIGURES 20 to 25. The largest adult leaves are those of *C. indivisa* (represented in FIGURE 22 on a smaller scale than the leaves of other species) and may exceed a meter in length. They develop a thickened fleshy base. Leaves of other species differ largely in the width of the blade and in whether they have a conspicuous grooved petiole (e.g. FIGURE 21) or not (e.g. FIGURE 24). Leaf shape differs considerably in different cultivars of *C. terminalis*; the series shown in FIGURE 25 is only a small sample but still shows almost the complete range of adult leaf shape for the genus as a whole. Varieties of *C. stricta* also differ markedly in the morphology of the adult leaf (FIGURE 20). This range of variation in both species includes leaves with and without grooved petioles.

Leaves of *Cordyline* are of interest to the comparative morphologist because, within the one genus, they show a range from linear, undifferentiated leaves to those in which there is a sharp differentiation between petiole and blade. However, a pronounced sheathing base is never developed so that although the leaf insertion is encircling it is never overwrapping.

FLOWERING

A brief description of inflorescence morphology and structure will serve to introduce the topic, although it is largely outside the scope of the present study. Flowering of *Cordyline* in New Zealand is clearly seasonal, from October to December, and seasonal flowering may be universal in the genus.

Inflorescence morphology. Inflorescences are terminal panicles with the same simple principles which underlie the construction of flowering axes in all woody monocotyledons. In the transition to the reproductive stage the main axis of the shoot elongates (FIGURE 26) and there is a rapid transition from normal foliage leaves to reduced leaves (bracts) which subtend the first-order branches. These branches repeat the structure of the main axis (FIGURES 27 to 29) often with branches of a second, but rarely of a third order. Bracts are progressively smaller in a distal direction on main axis and branches. The first leaf on each first-order branch is always a bicarinate prophyll, inserted basally. The prophyll subtends one or two buds, each in the angle of one of the keels. One or both prophyllar buds may grow out so that apparent clusters of first-order branches may develop; this tends to be a character of the *Cordyline* inflorescence.

Different species can be distinguished by the shape of the expanded inflorescence. This is largely determined by the number and density of branches which in turn is related to the phyllotactic arrangement on the parent shoot. This shape is represented diagrammatically by the inset figures for each species in the habit drawings (FIGURES 12 to 18).

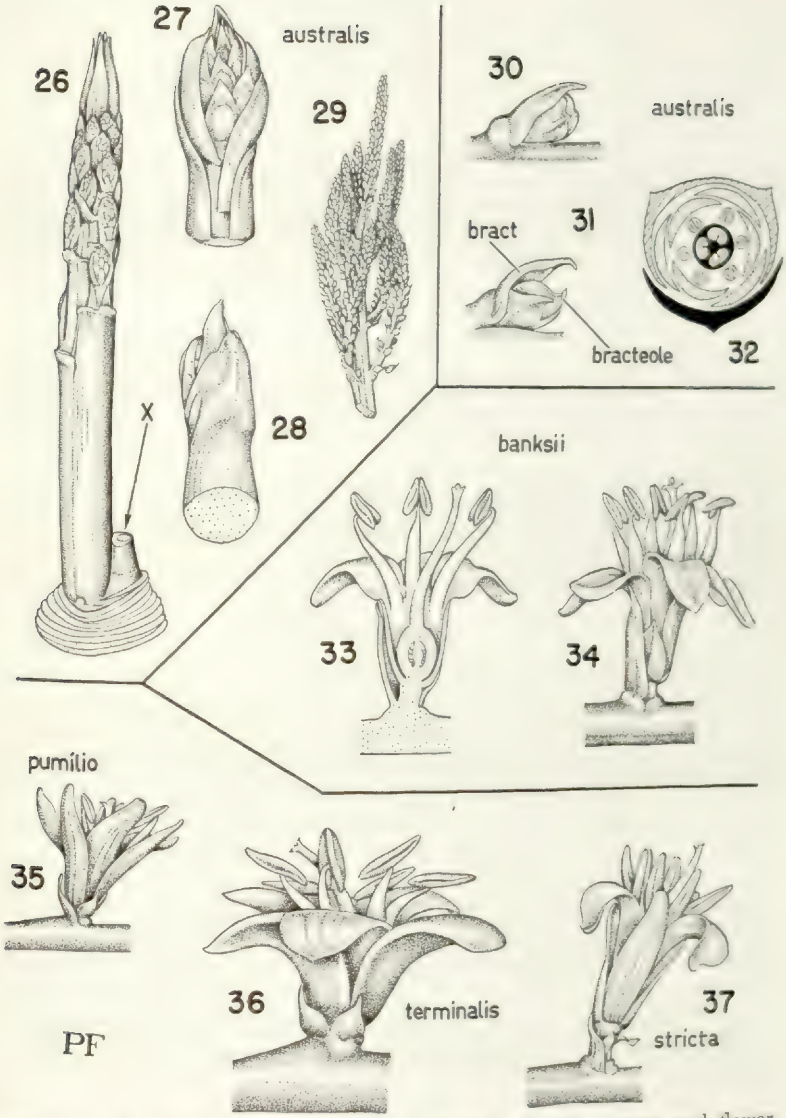
In *Cordyline australis* (FIGURE 18), *C. indivisa* (FIGURE 16), and *C. kaspar* (FIGURE 14) the inflorescence is much branched and congested. In *C. banksii* (FIGURE 12), *C. stricta* (FIGURE 13), and *C. terminalis* (FIGURE 17) the inflorescence is little branched and lax. *Cordyline pumilio* (FIGURE 15) has the most lax inflorescence and the longest peduncle, characters no doubt related to the habit of the species. Inflorescences of all these species are more or less erect initially but become pendulous with age, especially in *C. indivisa* (FIGURE 16). The inflorescence remains erect in *C. pumilio*.

The arrangement of first-order branches on the inflorescence continues the leaf arrangement of the vegetative shoot, so that it is spirodistichous in one group of species (*banksii*, *pumilio*, *stricta*, and *terminalis*) and spiral in the other (*australis*, *indivisa*, *kaspar*). This, in part, accounts for the difference in density of inflorescence branches in the two groups.

Floral morphology. Flowers occur singly in the axil of a bract (FIGURES 30 to 37). Each is subtended by a bracteole which is continuous and 2-keeled around the flower bud (FIGURES 30 to 32) but ruptures as the flower expands (e.g., FIGURE 36). Brown (1914) described the two split halves of the bracteole as two separate structures and emphasized this as a character diagnostic for *Cordyline*. Study of flower development in *C. australis* shows that this interpretation is incorrect because the bracteole is initiated as a single adaxial organ. Flowers of four different species are shown in FIGURES 33 to 37. The basic construction is uniform (FIGURE 32) but different species show slight quantitative differences. The relative lengths of members of the inner and outer perianth whorls, together with the length of the perianth tube have been accorded major diagnostic significance by earlier authors (e.g., Baker, 1875; Brown, 1914) but these characters seem difficult to apply and often are not very clear cut. Flowers are white or streaked with lilac in most species, but blue in *C. stricta*.

DISCUSSION

A peculiarity of the sapling stage of development in *Cordyline* is the positively geotropic rhizome which eventually appears as a continuation of the main axis. The biological function of this organ is evidently that of a "tap root," penetrating the substrate deeply and producing numerous adventitious roots over its surface. The inability of monocotyledons to develop a tap root is familiar and is a consequence of the inability of roots in monocotyledons to develop secondary vascular tissue and so to thicken with age. The only known exception to this generalization is *Dracaena*, where roots do undergo secondary thickening, although tap roots are not known in this genus. There are older descriptions of rhizomes in *Dracaena* (e.g., Velenovský, 1907; p. 375) but it is probable that these refer to misidentified species of *Cordyline*. We have already commented on this taxonomic confusion. The transformation of a stem into an organ with a root-like function as an interesting property of *Cordyline* was appreciated



FIGURES 26–37. **Cordyline** species, morphology of inflorescence and flower. 26–29, *C. australis*, young inflorescence: 26, entire terminal inflorescence at an early stage of development, dissected from the leafy crown, × 1/2; the continuing lateral renewal shoot, with apex cut off, is shown at X; 27, one first order branch from the same specimen, shown from the front. × 1 1/2; 28, the same, from the back, × 1 1/2; 29, part of a first order branch from an older specimen, at the time the inflorescence is exposed. × 1/2. 30–32, *C. australis*, floral morphology: 30, young flower bud enclosed by bract and bracteole. × 3; 31, the same, with flower bud removed. × 3; 32, floral diagram, with bract solid black, bracteole hatched. 33 and 34, *C. banksii*, flower, × 3; 33, longitudinal section; 34, from the side. 35–37, flowers shown from the side, × 3: 35, *C. pumilio*; 36, *C. terminalis*; 37, *C. stricta*.

by Goebel (1905) and Lindinger (1908). Comparable examples are found in *Dioscorea* and some species of *Costus* (Holttum, 1955).

The sapling stage of development of *Cordyline* (FIGURE 8) also offers the interesting situation of an axis with a shoot apex at each end, an unusual structure which has been commented upon by Troll (1937; p. 722). The hormonal balance in this axis is undoubtedly peculiar.

In the continuing investigation of *Cordyline*, structure and development of the vascular system in the axis are being examined. A comparative survey of leaf anatomy may help in solving some of the evident taxonomic puzzles in the genus. *Cordyline terminalis* has been selected as a subject for detailed study because it offers itself as an object for morphogenetic experiment. The questions to be answered include: under what circumstances does a bud develop as a rhizome or a leafy shoot? Under what circumstances does a rhizome become transformed into a leafy shoot? What determines the distribution of secondary tissues in these organs? Future reports will describe the variety of shoot expression in this species and the results of surgical and hormonal experiments which throw some light on these problems.

SUMMARY

An introduction to the morphology and development of the genus *Cordyline* (Agavaceae) is made with reference to seven species, mostly native to New Zealand, which have been studied as natural populations. Germination of seeds may be epigeous or hypogeous, depending on the species, and is followed by the growth of a positively geotropic rhizome from an axillary bud on the seedling axis. This replaces the first-formed part of the seedling axis. In this way a structure which has the function of a tap root is developed from an organ which is morphologically a stem. The subsequent diversity of habit in the adult stage of different species is described in relation to this seedling whereupon it is demonstrated that *C. pumilio*, a dwarf species, may be regarded as a neotenous form of larger, tree-forming species. A brief comparative account of phyllotactic pattern, leaf and inflorescence morphology is provided. This information provides a starting point for future descriptive and experimental studies on the morphology and anatomy of the genus.

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APPENDIX

SOURCES OF MATERIAL OF CORDYLINE EXAMINED:

C. australis	Waitakere Hills and Bethells Beach Road, North Island, New Zealand
C. banksii	Waitakere Hills, North Island, New Zealand
C. indivisa	Tongariro National Park, North Island, New Zealand
C. kaspar	Cultivated, Auckland, North Island, New Zealand
C. pumilio	Whangaparoa Peninsula, North Island, New Zealand
C. stricta	Cultivated, Auckland, North Island, New Zealand
C. terminalis	Cultivated, Miami, Florida, U.S.A., together with populations in New Guinea and Fiji.

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THE SAURURACEAE IN THE SOUTHEASTERN UNITED STATES[1]

CARROLL E. WOOD, JR.

SAURURACEAE E. Meyer, De Houttuynia atque Saurureis 20. 1827, "Saurureae," nom. cons.

(LIZARD'S-TAIL FAMILY)

A small, well-marked family of rhizomatous or stoloniferous herbs of wet habitats characterized by their simple, alternate leaves; ethereal oil cells in stems and leaves; racemose to spicate inflorescences terminal and/or opposite the leaves; small, perfect flowers lacking a perianth; [3 or] 6 hypogynous to epigynous stamens; small monocolpate pollen; nearly apocarpous [to syncarpous] gynoecium of 3 or 4 carpels with as many styles; [1,] 2 [or more] marginal [basal or parietal] orthotropous ovules in each carpel; and seeds with abundant perisperm, little endosperm and a minute embryo. TYPE GENUS: *Saururus* L.

Five genera (including seven species) of Asia and North America. The least specialized genus, *Saururus*, includes one species of eastern North America and one of eastern Asia; *Gymnotheca* Decaisne comprises two species of southern and western China and Indochina; while *Circaeocarpus* C. Y. Wu, known from southeastern Yunnan and northern Vietnam. *Houttuynia* Thunb., distributed from Japan to southern China and the Himalayas, and the greatly modified *Anemopsis* Hook. & Arn., of the southwestern United States and Mexico, are monotypic.

The genera show many close and reticulate relationships, and the six species demonstrate well evolutionary changes by reduction, connation, and adnation of floral parts. In both species of *Saururus*, the four carpels are united only at the base; in *S. cernuus* L. the six stamens are hypogynous, while in *S. chinensis* (Lour.) Baill. they are adnate to the lower part of the ovaries. In *Circaeocarpus saururoides* C. Y. Wu the three or four carpels are united, the ovary is one-locular with a single ovule,

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I am grateful to Dr. Shiu-Ying Hu for her translation from Chinese of some of the information pertaining to *Circaeocarpus*. The illustration was made by Arnold D. Clapman from materials collected by Dr. R. B. Channell and the late Dr. H. F. L. Rock and by Dr. K. A. Wilson and me. Items "g" and "h" in the illustration are after D. S. Johnson in Bull. Torrey Bot. Club 27: *pl.* 23. 1900.

and the six stamens are hypogynous. In *Gymnotheca*, the four carpels are united, the ovary is one-locular with four parietal placentae, and the six stamens are epigynous. In *Houttuynia cordata* Thunb. and *Anemopsis californica* (Nutt.) Hook. & Arn. the carpels are reduced to three and the ovary, three-locular above, one-locular below, has three parietal placentae. The three stamens of *Houttuynia* are perigynous, the six of *Anemopsis* epigynous. The bract subtending each flower shows elaboration and adnation to various degrees. In *Saururus* the small bract is adnate to the pedicel; in *Circaeocarpus*, *Gymnotheca*, and *Houttuynia*, it is free; and in *Anemopsis* it is adnate to the ovary and appears to be epigynous. In *Saururus*, *Circaeocarpus*, and *Gymnotheca chinensis* Decaisne the bracts are inconspicuous, but those of the lowermost three or four flowers of the open spike of *G. bracteata* P'ei are petaloid and white. The bracts of the short spikes of *Houttuynia* and those of the lowermost six to eight flowers of the condensed spikes of *Anemopsis* are petaloid, white, and appear to form an involucre, the whole inflorescence in *Houttuynia* and *Anemopsis* simulating a flower of the type of *Anemone virginica* L. The adnation of stamens and ovary seen in *Saururus chinensis*, *Houttuynia*, and *Gymnotheca*, is climaxed in *Anemopsis* by the adnation of both stamens and bract to the ovary and by the lateral developmental concrescence of the ovaries of individual flowers, giving the appearance of a "sinking" of the flowers into the inflorescence axis.

Engler regarded the Saururaceae as the most primitive family of dicotyledons after the Casuarinaceae but all evidence points toward simplicity through reduction. It has also been suggested on the basis of the structure in *Saururus cernuus* that the flower is not actually simple but is derived by condensation of an inflorescence. Each flower would then be represented by a carpel with its own stamen or stamens. (Cf. Raju.)

The accumulating evidence suggests that the Saururaceae and Piperaceae are most closely related to each other and that they fall within the group of ranalian families with monocolpate pollen (or phylogenetically derived types), ethereal oil cells, and trilacunar or multilacunar nodes, among which they are the most specialized members. Although the Chloranthaceae have also been associated with Piperaceae and Saururaceae, Swamy has shown that "the Chloranthaceae exhibit significantly diverse trends of phylogenetic modification as compared with Piperaceae and Saururaceae," and that they probably should be allied with the group of ranalian families with monocolpate pollen, ethereal oil cells, and unilacunar nodes.

The best-studied member of the family is *Houttuynia cordata* (see references). It is a long-day plant, flowering with 14 or more hours of light. The plagiotropic growth of the rhizome is controlled by the leaves: one-half of a leaf suffices; if all are removed from the nearest erect shoot, the tip of the rhizome grows upward, becoming an aërial shoot. Meiotic irregularities leading to a high degree of pollen sterility, diploid embryo sacs, and parthenogenesis have been reported in this species, which appears to be polyploid ($2n = 96$).

The development of both male and female gametophytes is quite similar in *Saururus*, *Houttuynia*, and *Anemopsis*, and in all the embryo sac development is of the normal (Polygonum) type. The endosperm is of the cellular type. A conspicuous haustorial cell which persists in the ripe seed is formed by the first division of the endosperm nucleus (see FIGURE 1, g).

The group is of little economic importance. *Saururus cernuus* may be weedy, and its dense growth may favor the breeding of anopheline mosquitoes; *Houttuynia* can be an obnoxious weed. The strong-flavored shoots of *Houttuynia* are eaten as a vegetable in China, and both this and *S. chinensis* are used in Chinese medicine.

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1. **Saururus** Linnaeus, Sp. Pl. 1: 341. 1753; Gen. Pl. ed. 5. 159. 1754.

Emergent aquatic perennial herbs of shallow, standing or slow-moving waters. Rhizomes subterranean, horizontal, white, branching. Roots fibrous, triarch to pentarch, adventitious at submerged nodes, lacking root hairs. Leafy stems erect, 7–9-furrowed, with 20–30 vascular bundles in a single ring and 7 or more cortical bundles. Leaf blade cordate, ± palmately veined; petiole with 7–9 vascular bundles, sheathing at the base (sheath apparently produced by the adnate stipules). Leaves and stems aromatic when crushed. Inflorescences 1–6 long-pedunculate, dense, 200–350-flowered spikelike racemes terminal and/or opposite the leaves (sympodial), drooping at anthesis, gradually becoming erect as flowering proceeds, erect in fruit. Flowers perfect, fragrant, spirally arranged on the white axis, the pedicel adnate to a light-green subtending boat-shaped bract, the flower then appearing to be sessile on the bract. Stamens 4–8, typically 6, hypogynously [or perigynously] and spirally inserted, but in ours often appearing to be 3 each on the ad- and abaxial sides of the gynoecium; filaments conspicuous, white, capillary, much exceeding the gynoecium [or inconspicuous and much shorter than the gynoecium], tapering abruptly into the light-yellow basifixed elliptical anthers; anthers 4-locular, 2-locular at anthesis, opening by longitudinal slits. Gynoecium 3–5 (typically 4)-carpellate, the carpels spirally arranged, conduplicate, not sealed above the placental area, syncarpous at the base; stigmas 2-crested, decurrent along the edges of the short, recurved, adaxially grooved style; each carpel with a single orthotropous 2-integumented, crassinucellate ovule on the inner edge of each half near the adaxial suture, one ascending, the other transverse below it, only the ascending one developing into a seed. Carpels becoming wrinkled and warty in fruit,

indehiscent, separating at maturity, the styles persistent. Seed solitary, with a pale, filmy outer coat and a hard, brown inner coat; perisperm massive, filling most of the seed; endosperm at the micropylar end of seed surrounding the minute, poorly differentiated embryo. (*Spathium* Loureiro, *Mattuschkia* Gmelin, *Saururopsis* Turcz., *Neobiondia* Pamp.) TYPE SPECIES: *S. cernuus* L. (Name from Greek, *sauros*, lizard, and *oura*, tail, from the appearance of the inflorescence of *S. cernuus*.) — LIZARD'S TAIL.

Two species, *Saururus cernuus*, $2n = 22$, in eastern North America, and *S. chinensis* (Lour.) Baill. (*S. Loureiri* Decaisne, *Spathium chinense* Lour.),

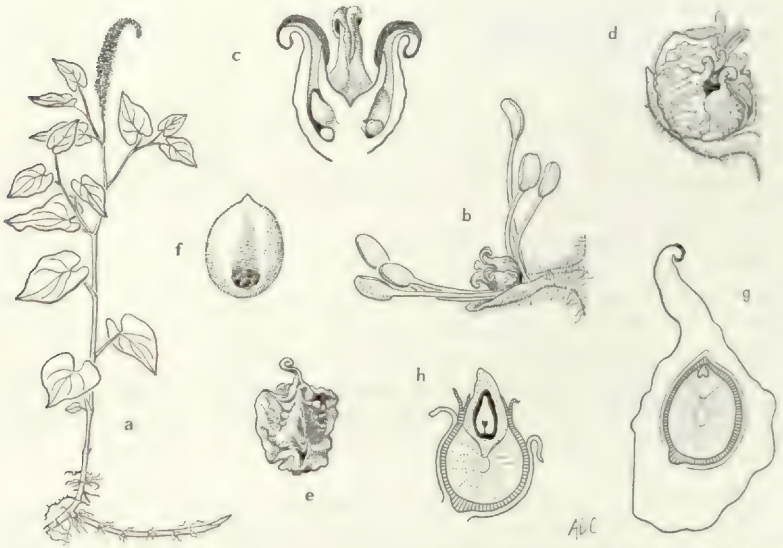

FIGURE 1. **Saururus.** a–h, *S. cernuus*: a, habit, showing erect flowering shoot and horizontal rhizome, × 1/8; b, flower, pedicel, and bract, × 5; c, gynoecium in vertical section — note stigmatic crests, ascending ovule in carpel at left, horizontal ovule in section, and horizontal ovule in right-hand carpel, the ascending ovule on removed carpel-half, × 18; d, nearly mature but still green fruit, × 5; e, mature dry fruit, adaxial surface, × 8; f, seed from same after soaking, × 12; g, carpel and seed in diagrammatic vertical section, showing outer seed coat (white), hard inner seed coat (hatched), perisperm (curved unstippled lines), endosperm (even stipples), endosperm haustorial cell (unshaded), and minute embryo, × 18; h, germinating seed in diagrammatic vertical section, × 18.

$2n = 22$, in eastern Asia, ranging from Indochina and southern and central China to Taiwan, the Philippines, and Japan. *Saururus cernuus* grows in swamp forests, marshes, ponds, and sluggish streams in 5 to 45 cm. of water over a wide area from southernmost peninsular Florida, westward to Texas, and northward to Rhode Island, Connecticut, southwestern Quebec, southern Ontario, central Michigan, Illinois, Missouri,

and southeasternmost Kansas and Oklahoma. Although mostly restricted to low altitudes, it apparently is tolerant of a wide range of pH and temperatures.

Spreading by rhizomes, *Saururus cernuus* forms dense colonies that compete successfully with other emergent aquatics. In a study in Tennessee, Hall estimated that the aërial stems from a square foot of ground in a dense colony bore 13 square feet of leaf surface, while the total length of rhizomes was 13 linear feet. Seed production for the same area was estimated at 20,000, but no seedlings were seen anywhere. The fruits and the fragmented rhizomes presumably are distributed by water (although about 95 per cent of the fruits sink within three hours). Johnson found that a dormant period apparently independent of temperature is necessary for seed germination. In germination the endosperm bursts through the seed coats at the micropylar end, projecting as a white papilla. The embryo, still quite rudimentary, then begins to develop, the hypocotyl first pushing through the tip of the endosperm and eventually only the ends of the cotyledons remaining within the endosperm, which serves as a digestive organ to absorb the food reserves of the perisperm filling most of the seed.

Baldwin & Speese suggest that *Saururus cernuus* would be excellent for teaching purposes, since the meiotic divisions of the pollen mother cells are especially clear and all stages are found in the anthers of a single flower. Thirteen chromosome counts (made from very young leaves) representing 12 widely scattered localities all showed $2n = 22$.

The four carpels of *Saururus cernuus* are arranged spirally, and the carpellary vascular bundles originate spirally. The first formed carpels usually have two stamens each, while the last (fourth) does not have one associated with it.

The genus is characterized by pedunculate racemose inflorescences without enlarged bracts at the base; flowers typically with four nearly free carpels, each with two ovules; six hypogynous to perigynous stamens; and wrinkled, indehiscent one-seeded fruits. The flowers of *Saururus cernuus*, with their long, white, hypogynous staminal filaments much exceeding the gynoecium, are quite conspicuous, while those of *S. chinensis*, arranged in a more open erect inflorescence, are less so, being smaller, yellowish or whitish, with the stamens shorter than the gynoecium and adnate to the base of the ovaries. The uppermost leaves of *S. chinensis*, however, may be partly or completely white, functioning in the attraction of insects. The flowers of both species are fragrant. Baillon placed *S. chinensis* in a separate section, SPATHIUM (Lour.) Baill.

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A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR *

S. M. A. KAZMI

3. **A. euchroma** (Royle) I. M. Johnston, Contr. Gray Herb. **73**: 49. 1924; Riedl in Rechinger, Fl. Iranica **48**: 164. 1967.

Lithospermum euchromon Royle, Illustr. Bot. Himal. Mount. **1**: 305. 1839.
Stenoselenium perenne Schrenk ex Fisch. & C. A. Mey. Enum. Pl. Schrenk **1**: 34. 1841.
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Munbya perennis (Schrenk) Boiss. Diagn. Pl. Orient. **11**: 115. 1849.
Macrotomia endochroma Hook. f. & Thoms. ex Henderson & Hume in Lahore to Yarkand 328. 1873; Aitchison, Jour. Linn. Soc. **18**: 81. 1880; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 177. 1883, *in syn., nomen nudum.*
Macrotomia perennis (Schrenk) Boiss. Fl. Orient. **4**: 212. 1875.
Macrotomia onosmoides Regel & Smir. Acta Horti Petrop. **2**: 624. 1878.
Macrotomia euchroma (Royle) Paulsen, Bot. Tidskr. **27**: 216. 1906; Stud. Veg. Pamir 58. 1928; Lipsky, Acta Horti Petrop. **26**: 505. 1910.
Macrotomia euchroma var. *subacaulis* Lipsky, Acta Horti Petrop. **26**: 510. 1910.
Macrotomia oginoi Kitamura, Act. Phytotax. Geobot. **19**: 104. 1963.
Arnebia euchroma subsp. *caespitosa* Rech. f. & Riedl, Oesterr. Bot. Zeitschr. **111**: 152. 1962; Riedl in Rechinger, Fl. Iranica **48**: 166. 1967, *syn. nov.*

TYPE: India: Naho in Kunawur, *Royle s.n.* (K).

ICON.: Paulsen, l. c. *fig. 20.* 1928, under *Macrotomia euchroma.*

Perennial, erect, caespitose herb with thick roots rich in purple dye, sometimes to 2 cm. in diameter. Stems many, arising from the axils of the leaves, which formed a sterile basal cluster the preceding year, unbranched, pale to brownish purple, fistulous, ± striate, to 50 cm. long, covered sparsely or densely with white, thin to thick trichomes, to 2 mm. long with minute to large tuberculate bases. Primary basal leaves lanceolate, entire, acute, attenuate towards the broad, ciliate base, usually imperfectly developed and much smaller than the secondary leaves; secondary basal leaves lanceolate, tapering towards the acute apex, more gradually narrowed into a short, winged, dilated, ciliate base, with one strong prominent rib, to 11 cm. long, 15 mm. broad, sparsely to densely covered on both surfaces with white thick or thin, spreading or subappressed trichomes, to 2 mm. long, with tuberculate bases; lower middle cauline leaves sessile, lanceolate, broadest in the middle of the lower half, then gradually narrowed through the elongate upper half to an acute apex, rounded or subtruncate at the base, to 8 cm. long, 15 mm. broad; upper cauline leaves usually shorter and broader, apex more elongate, rounded to

* Continued from volume 52, p. 363.

sometimes subcordate at the base. Inflorescence terminal, subglobular, tending to become broader than long, not elongated in fruit, 5–6 cm. in diameter, bracteate, bracts short, leaflike, not exceeding the calyces. Pedicels erect, densely hairy, very short in flower, to 5 mm. long in fruit. Calyx divided to the base, lobes hairy, linear-lanceolate, acute, to 10 mm. long, 1.5 mm. broad in flower, enlarged to 20 mm. long, 3 mm. broad in fruit. Corolla purplish-white, purple or brownish-purple, funnelform, 16–22 mm. long, tube 10–15 mm. long, limb 5–7 mm. long and 8–16 mm. in diameter, divided nearly one-half its length, lobes ascending, suborbicular to ovate, throat usually glandless, appendages lacking, but in long-styled flowers occasionally developing 5 small, weakly invaginated swellings, nectary not developed. Anthers borne either at the middle or at the summit of the corolla tube. Style reaching the middle of the tube or slightly exserted, usually forked at the apex; stigmas 2, compressed, rounded, broader than long. Nutlets gray, dusky, irregularly and coarsely tuberculate and more or less rugose, surface dull, covered with microscopic papillae, broad near the middle, 3–4 mm. long, with a well developed keel on the venter, which extends to the beaked apex and continues down the back side, attachment scar flat and frequently bearing 2 ventral traces.

DISTRIBUTION: Iran, Afghanistan, West Pakistan, Kashmir, northwest India to Nepal, Turkestan, Pamir Alaj.

3a. Var. euchroma.

Plants less pungently hirsute, having narrower cauline leaves, truncate or roundish at base and less acute at apex in comparison with those of *Arnebia euchroma* var. *grandis*.

West Pakistan: CHITRAL STATE: Haute vallée de Yarkhun, 4000 m., *Schmid 2285* (BM, G), upper Yarkhun Valley, *Schmid s.n.* (MICH); Chitral Gol, left of Chitral, 3300 m., *Stainton 2696* (BM); Turikho River, Istar, 3000 m., *Stainton 2487* (BM); Birmogh Lasht, 3300 m., *Bowes Lyon 735* (BM). GILGIT AGENCY: Baltistan, upper end of Hushe Valley, Chogolisa Glacier, 3500 m., *Webster & Nasir 6001* (GH); Chalpani Nala, *Duthie 13855* (BM, E); Turmih Nullah, 3000 m., *Ludlow 299* (A, BM); Naltar Lakes, 3500 m., *R. R. Stewart 26328* (BM); Deosai Pass from Minimarg, 3300 m., *R. R. Stewart 22171* (GH); Satpura Nullah above Skardu, 3000 m., *R. R. Stewart 20289* (GH); Karakorum Expedition 1939, Hispar Glacier, east of Sekambarisi Glacier, 4000–4500 m., *Russell 1494* (BM); 4000 m., *Russell 1535* (BM); Gharesa Glacier, slopes of Buri Harar, 4500 m., *Russell 1138* (BM); Baifa Glacier, left bank, 4500–4700 m., *Russell 1825* (BM); north of Hindukush, *Giles s.n.* (E). HAZARA DIST.: Kaghan Valley, 4 miles beyond Burawai, *Burtt B932* (E). KURRAM AGENCY: Kurram Valley, *Aitchison 498, 824* (G). QUETTA DIST.: Zarghum, *Lace 3760* (E).

Kashmir: Dras Valley, 3000–3300 m., *Duthie 11695* (E); between Dras and Pindras, 3000 m., *Dickason 84* (MICH); southwest of Dras, Mitsahoi-Matayan, 3000 m., 88 road-miles east-northeast of Srinagar, *Dickason 85* (MICH); Matayan-Mitsahoi, Ladak Road, 3100 m., *R. R. Stewart 10004* (GH); Dras, Ladak Road, 300 m., *R. R. Stewart 10055* (GH); Zanskar, Chumik Marbo, 4300 m., *Koelz 5381* (GH, MICH, US); Tsanskar, Pader on the northern foot of the Shin-

kula Pass to Súlle, *Schlagintweit 6258* (GH); Kargia, 3300 m., *Koelz 5460* (GH, MICH, US), *5553* (MICH, US); Bok, Pasni La, 5000 m., *Koelz 5834* (GH, MICH, US); Zoji La, 3000 m., *Ludlow & Sherriff 8311* (GH). Miscellaneous: Tibet occ., 14,000–16,000 ped., Herb. Ind. Orient. Hook. f. & Thoms., *Thomson s.n.* (GH-isotype of *Macrotomia endochroma*).

3b. Var. **grandis** (Bornm.) Kazmi, comb. nov.

Macrotomia grandis Bornmüller, Oesterr. Bot. Zeitschr. **47**: 289. 1897.
Arnebia euchroma (Royle) I. M. Johnston subsp. *grandis* Riedl, Oesterr. Bot. Zeitschr. **111**: 152. 1964; in Rechinger, Fl. Iranica **48**: 166. 1967.

TYPE: PERSIA: Kerman, Kuh-e-Laheh Zar, 3600 m., *Bornmüller 3948* (W-holotype, GH-isotype).

Plants more pungently hirsute, having broader cauline leaves, obviously subcordate at base, abruptly narrowed in the upper half into a long acuminate tip.

DISTRIBUTION OF VARIETY: Iran.

Arnebia euchroma is very variable in the size and indumentum of the leaves, in the density and length of trichomes and the size of their basal tubercles, as well as the length of corolla and calyx.

The primary basal leaves are small and usually imperfectly developed whereas the secondary basal leaves are well developed and reach 11 cm. in length and to 1.5 cm. in width. Usually the primary leaves disappear on the emergence of the secondary leaves. The cauline leaves are more stable in their shape compared to the basal ones. The latter have broad sessile bases, broadest at the middle of the lower half, then becoming gradually narrowed to acute apices. Only in few specimens from Tibet and Lahul (in northwestern India) were the bases of the cauline leaves found to be slightly subcordate. The trichomes on both surfaces of the leaves vary greatly in their density, the length and the size of their basal tubercles, and whether they are erect or subappressed. I could not establish any correlation between the ratio of corolla and calyx length and the variations in the leaf-size and the type of trichomes borne. Only in a few specimens from Chitral are the cauline leaves narrower compared to those of the specimens from other parts of West Pakistan, Afghanistan and Kashmir. But such plants are also not rare in the collections from Nepal, the easternmost limit of distribution of *A. euchroma*.

The only variation worth recognition is var. *grandis*, based on Bornmüller's collection from Iran, which can be distinguished from the typical variety by being pungently hirsute and having cauline leaves much broader at base, evidently subcordate and abruptly narrowed into a long-acuminate apex.

4. **A. inconspicua** Hemsl. & Lace, Jour. Linn. Soc. Bot. **28**: 326. 1891; Riedl in Køie & Rechinger, Biol. Skr. 13(4): 240. 1963, in Rechinger, Fl. Iranica **48**: 166. 1967.

Arnebia argyrea Rech. f. Ann. Naturh. Mus. Wien **58**: 59. 1951.
Lithospermum inconspicuum (Hemsl. & Lace) I. M. Johnston, Jour. Arnold Arb. **34**: 12. 1953.
Macrotomia inconspicua (Hemsl. & Lace) Kitamura, Fl. Afghanistan 321. 1960.

TYPE: BALUCHISTAN: Zarghum, at 9500 ft., 1. 5. 1888, *Lace 3759* (E-holotype).

ICON.: Riedl, l. c. *fig. 187–189*. 1963.

Erect perennial herb with a woody rootstock formed of crowded branches, ensheathed by old leaf-bases, from a deep dye-stained root with easily peelable bark. Stem usually solitary, arising from the center of the leaf-rosette, unbranched, 5–15(–25) cm. tall, covered densely with appressed, silvery trichomes, not tuberculate at bases, to 0.5 mm. long, intermixed profusely with spreading, thick, stiff, pungent, white trichomes, to 2 mm. long. Basal leaves linear to linear-lanceolate, entire, sometimes slightly revolute at margins, acute with a prominent midrib below, covered with trichomes like those of the stem, 3–7 cm. long, 3–5 mm. broad; cauline leaves few, sessile, shorter and narrower. Inflorescence capitate, globular, 3–5 cm. in diameter, slightly elongated in fruit; bracteate, bracts linear; rarely a small cluster of cymes is developed in leaf-axils below the major cluster. Calyx divided nearly to the base, lobes subulate-linear, more or less equalling the corolla tube, 10–16 mm. long, ± 1 mm. broad at base, not elongated in fruit. Flowers heterostyled. Corolla whitish to yellow, sometimes purplish-yellow in dried specimens, narrowly tubular, externally hairy, trichomes appressed, glabrous within with few scattered trichomes on the lobes, 12–19 mm. long; tube 9–12 mm. long, throat funnelform, somewhat glanduliferous, short, 2 mm. long in short-styled flowers; tube 12–14 mm. long and 2 mm. thick at base, 1–1.5 mm. above the base, and above very gradually broadening into the throat in long-styled flowers; limb ascending, 2.5–4.5 mm. in diameter, lobes triangular-ovate, acute, 1–2 mm. long. Anthers 2 mm. long; filaments very short, inserted either above the middle of the corolla tube or on the throat. Style forked, branches slightly unequal, reaching the middle or up to the throat of the corolla tube, stigmas 2, distinct, compressed, nearly as long as broad. Usually one nutlet developed, ovate, indistinctly beaked, dorsally and ventrally keeled, smooth, shining, ± 5 mm. long.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: QUETTA DIST.: Zarghun, 2800 m., *Lace 3759* (E); Zahru, *Stocks 866* (K-in part); Quetta to Ziarat, at the top of Pass, 2500 m., *Lamond 1176* (E); *Kazmi 1663b* (PES); in montibus S.W. Ziarat, 2200–2500 m., *Rechinger 29346* (G, W). Miscellaneous: Without locality, 1891–1894, *Elliot s.n.* (K).

5. **A. hispidissima** (Lehm.) A. DC. in DC. Prodr. **10**: 94. 1846; Jaub. & Spach, Illustr. Fl. Orient. **4**: 100. 1852; Boiss. Fl. Orient. **4**: 213. 1875; C. B. Clarke, Jour. Linn. Soc. Bot. **18**: 524. 1881; in Hook. f.

Fl. Brit. India 4: 176. 1883; Riedl in Rechinger, Fl. Iranica 48: 155. 1967.

Anchusa hispidissima Sieber ex Lehm. Icon. 1: 23. 1821, *in synon.*
Anchusa asperrima Delile, Fl. Aegypt. Illustr. 7. 1813, *nomen nudum.*
Anchusa polygama Hamilton ex G. Don, Gen. Syst. 4: 325. 1837, *in synon.*
Arnebia asperrima (Del.) Hutch. & Dalz. Fl. W.-Afr. 2: 201, 608. *fig. 246.* 1931.
Arnebia lutea (A. Rich.) Armori in Pirotta, Ann. Ist. Bot. Roma 8: 161. 1904.
Arnebiola migiurtina Chiov. Fl. Somala, 227. *t. 24, fig. 1.* 1929.
Arnebia purpurascens (A. Rich.) Baker, Fl. Trop. Afr. 4: 56. 1906.
Dioclea hispidissima (Sieber) Spreng. Syst. Veg. 1: 556. 1825.
Echiochilon hispidissima Tausch, Flora 12: 643. 1820.
Echiodes asperrima (Del.) Rothm. Repert. Sp. Nov. 49: 56. 1940.
Lithospermum hispidissimum Lehm. Icon. 1: 23. *t. 39.* 1821.
Lithospermum vestitum Wall. Cat. No. 941. 1829, *nomen nudum*; Benth. in Royle, Illustr. Himal. Mount. 305, 1836; G. Don, Gen. Syst. 4: 325. 1837.
Strobila hispidissima G. Don, *Ibid.* 327. 1837.
Toxostigma luteum A. Rich. Tent. Fl. Abyss. 2: 86. 1850. [1851 f. Pritzel.]
Toxostigma purpurascens A. Rich. *Ibid.* 87. *t. 77.* 1850. [1851 f. Pritzel.]

TYPE: AEGYPTUS: Wadi Gamuhs, *Sieber s.n.* (BM, GH, W).

ICON.: Wight, Icon. Pl. Indiae Orient. 4: *t. 1393.* 1848; Jaub. & Spach, l. c. 4: *t. 363.* 1852; Hutch. & Dalz. l. c. *fig. 246.* 1931, under *Arnebia asperrima.*

Erect or decumbent annual herb, with dye-stained tap root. Stems solitary to few, compactly branched; the whole plant covered with stout, white, pungent, spreading to rarely subappressed unequal trichomes with large tuberculate bases, the area between the tubercles usually densely covered with soft, nonpungent, usually antrorsely appressed or sometimes spreading white, nontuberculate trichomes, not exceeding 0.5 mm. in length, sometimes these areas puberulous or rarely quite glabrous. Basal leaves few to many, usually drying at anthesis, lanceolate, entire to crenulate or sometimes slightly revolute at margins, acute to subacute, attenuate towards the base, to 5 cm. long, 5 mm. broad; cauline leaves reduced in size upwards. Inflorescence of scorpioid cymes terminating the stem and numerous branches, simple and short in flower, later elongating to 20 cm., bearing closely set flowers or distant fruits, bracteate, bracts narrow to broadly lanceolate. Calyx sessile, divided to the base, lobes linear-lanceolate to lanceolate, acute, unequal, to 7 mm. long and 1.5 mm. broad in flower, not at all to slightly enlarged in fruit. Corolla yellow, densely villulose externally, villulose in a band near the base within, ca. 1 mm. broad, 10–15 mm. long, tube 7–13 mm. long, nectary very narrow, lobulate, sparingly villulose, throat glabrous, without glands or appendages, limb funnelform, 4–8 mm. in diameter, lobes roundish, spreading to suberect, 1–2 mm. long. Flowers heterostyled. Stamens attached at the middle of the upper quarter of the tube or at its summit, anthers 1.2–1.8 mm. long, filaments usually 0.9–1.2 mm. long. Style reaching the middle of the corolla tube or its summit or sometimes even exserted, forked, more

deeply so on the long styles; stigma reniform or in long-styled flowers flabellate-reniform and almost lobed. Nutlets pyramidal-ovoid, broadest at the base, pink to brown, nearly smooth to tuberculate, 1.5–2 mm. long.

DISTRIBUTION: north and east Africa, Arabia, Iran, West Pakistan and plains of northwest India.

West Pakistan: ATTOCK DIST.: Campbellpore, ca. 400 m., *Kazmi 228b* (PES). BANNU DIST.: between Sarai Naurang and Lakki Marwat, 3 miles from Sarai Maurang, *Kazmi 119a* (PES); Bannu to Miram Shah, near Mir Ali, *Kazmi 127a* (PES). CHITRAL STATE: Drosh, 1350 m., *Stainton 2254* (BM). DERA GAZI KHAN DIST.: 25 miles from Dera Ghazi Khan to Taunsa, ca. 300 m., *Kazmi 2566* (PES); 3 miles from Dera Ghazi Khan to Muzzafargarh, ca. 300 m., *Kazmi 2551* (PES). DERA ISMAIL KHAN DIST.: between Moghal Kot and Daraban, *Kazmi 1978b* (PES); Dera Ismail Khan, along the bank of Indus, *Kazmi 2479* (PES); 10 miles to Tank on Dera Ismail Khan-Tank road, *Kazmi s.n.* (PES); N. Dera Ismail Khan, *Rechinger 30024* (G, W). HAZARA DIST.: between Haripur and Hasan Abdal, *Kazmi 134b* (PES); Mansehra, *Kazmi 2491* (PES); HYDERABAD DIST.: 10 miles from Hyderabad towards Hala, *Kazmi 5459b* (PES); between Hyderabad and Tandu Mohammad Khan, *Kazmi 2542* (PES). JHELUM DIST.: Jhelum, *Iftakhar Ahmad 54* (MICH); 2 miles from Chakwal to Bhaun, *Kazmi s.n.* (PES); Chanuwala, north of Khewra, *Kazmi s.n.* (PES). KARACHI DIST.: Mauripur, *Kazmi 2532a* (PES); Drig Road, *Kazmi s.n.* (PES), *Jafri*, Dec. 1951, *s.n.* (E); Drig Road near Karachi, *Stearn 27* (K), *Jafri*, Sept. 1951, *s.n.* (E); Malir, *Jafri 2544* (E), *Tasnif 478* (PES); Jemindar ka Landa near Karachi, *Stocks s.n.* (K); Dabbeji, *Koelz 7596* (GH, MICH, US); inter Damloti et Khadeji, *Rechinger 28505* (G, W); *Lamond 745* (E); Manora, *Kazmi 2533a* (PES); between Sonmiani and Uthal, *Kazmi 882a* (PES). LAHORE DIST.: Lahore to Jaranwala, near Sharqpur, *Kazmi s.n.* (PES); Lahore to Raiwind via main highway, 10 miles to Raiwind, *Kazmi s.n.* (PES); Shahadra, near bridge, *Kazmi s.n.* (PES); Lahore, *R. R. Stewart 7091* (GH, K); May 1937, *H. Choudhri s.n.* (GH). MULTAN DIST.: Multan, *Kazmi s.n.* (PES). PESHAWAR DIST.: near Akora Khattak, between Noshehra and Khairpur, *Kazmi 486b* (PES). RAWALPINDI DIST.: Golra, *Kazmi 2522a* (PES); Texila, *Kazmi 2548* (PES). Miscellaneous: bank of Chenab, 1000 ped., Herb. Ind. Or. Hook. f. & Thoms., 1846, *Thomson s.n.* (GH, K); Punjab, *Drummond*, Kew Herb. No. 20708 (K); Scinde, *Stocks 417* (K); Herb. Late East India Co., *Falconer s.n.* (GH). Reported from: Kalat, Harboi, S.-E. Kalat, *Hotson 62*, Baluchistan, without locality, *Stocks s.n.*

Arnebia hispidissima is closely related to *Arnebia griffithii*, from which it is distinguished by being more bristly in habit and in having lanceolate, acute to subacute, shorter and narrower basal leaves. The calyx lobes in *A. griffithii* are equal in length, to 9 mm. long and 0.5 mm. broad, whereas in *A. hispidissima* these lobes are usually unequal in length, 7 mm. long, and to 1.5 mm. broad. The corollas in both the species are yellow, but those of *A. griffithii* have prominent dark purple spots at the sinuses of the corolla lobes. In *A. hispidissima* the corolla limbs are slightly zygomorphic, while in *A. griffithii* they are always regular. *A. hispidissima* has a glabrous corolla throat and the tube is minutely hairy in a band nearly 1 mm. broad within, which is not the case in any allied species.

Arnebia hispidissima has a wide distribution from Egypt to the eastern

Himalayas [*Griffith 5950* (GH)], and therefore the plants vary greatly in habit, apparently in response to the varying rigor of the habitat. The plants of the coastal and sandy dry areas are usually lower and more compactly branched, whereas those of the inland areas are usually erect with loosely ascending branches. The plants of Egypt, Arabia and those collected from the southern, sandy and dry parts of West Pakistan usually bear both types of trichomes, short ones without tuberculate bases and the very long, stout and pungent type with broad calcareous tuberculate bases. The short trichomes are usually lacking in the plants collected from the northern part of West Pakistan, Punjab, and Utter Pradesh provinces of India. In a few cases these plants have broader bracts.

6. **A. griffithii** Boiss. Diagn. Pl. Orient. **3**: 135. 1856; Fl. Orient. **4**: 213. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 176. 1883; Riedl in Rechinger, Fl. Iranica **48**: 156. 1967.

Echioides griffithii (Boiss.) Rothm. Repert. Sp. Nov. **49**: 56. 1940.
Lithospermum griffithii (Boiss.) I. M. Johnston, Jour. Arnold Arb. **33**: 326. 1952.

TYPE: Afghanistan, without locality, *Griffith 5953* (K-holotype, GH, W-isotypes).

ICON.: Hooker in Curtis's Bot. Mag. **87**: *t. 5266*. 1861.

Annual erect herb with slender roots slightly stained with purple dye. Stems pale brown, single to many, ascendingly branched, to 30 cm. long; usually densely, rarely sparsely covered with stiff, spreading, white trichomes, to 1.5 mm. long, usually arising from tuberculate bases. Basal leaves linear to oblong-obovate, entire, roundish, obtuse or rarely subacute at apex, gradually narrowed towards the base, to 7 cm. long and 1 cm. broad, covered on both surfaces and margins with spreading or subappressed trichomes like those of the stems, but usually with larger tuberculate bases; cauline leaves usually shorter and narrower, less attenuate towards the base. Inflorescence congested and short in flower, later elongated, bearing distant flowers or fruits, to 10 cm. long; bracteate, bracts hairy, linear, usually shorter than the calyx, to 15 mm. long, 1 mm. broad. Flowers sessile, fruits subsessile. Calyx divided to the base, lobes densely hairy, to 9 mm. long, 0.5 mm. broad, erect, enlarged and dilated at base in fruit, to 15 mm. long, 1 mm. broad. Corolla yellow or orange, 20–23(–30) mm. long, tube slender, much surpassing the calyx, 15–18 mm. long, limb spreading with five dark purple spots, 10–15(–20) mm. in diameter, lobes broadly ovate or roundish, entire at the margins, throat glabrous or scantily glanduliferous, without appendages, nectary a narrow villous collar. Flowers heterostyled. Stamens attached either just above the middle of the corolla tube or at the summit, and almost exserted. Style reaching to above the middle of the tube or to the summit, sometimes even slightly exserted, bifid; stigma compressed reniform or flabellate, entire or obscurely lobed. Nutlets trigono-pyramidal, brownish, more or

less lustrous, sparsely and coarsely tuberculate, back somewhat cordate at base, ca. 2 mm. long and broad at base.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: ATTOCK DIST.: *R. R. Stewart 27521* (BM); Campbellpore, *R. R. Stewart 15303* (GH), *Kazmi 2720* (PES); between Campbellpore and Grand Trunk Road, ca. 350 m., *Kazmi 2729* (PES); between Attock bridge and village, ca. 300 m., *Kazmi 2659* (PES). JHELUM DIST.: Salt Range, Chedroo, *Fleming 21* (E). KHYBER AGENCY: Jamrud, 400 m., *Kazmi 2693* (PES); between Jamrud and Landi Kotal, *Kazmi 2708* (PES); near Afghan border, *Rodin 5262* (US); Khyber Pass, near Zintara, *Burtt & H. H. Naira 580* (E); between Landi Kotal and Torkham, *Kazmi 2714* (PES); along road from Jamrud to Warsak, 300 m., *Kazmi 2697* (PES); Warsak, ca. 3500 m., *Kazmi 2702* (PES). KOHAT DIST.: between Matanni and Kohat, 300–400 m., *Kazmi 2628* (PES); north of Kohat, *Kazmi 2636* (PES); between Hangu and Kohat, ca. 300 m., *Kazmi 2626* (PES); between Kohat and Sulaiman Khel, *Kazmi s.n.* (PES); Khushalgarh, *Kazmi & A. J. Ahmad 2645* (PES); between Khushalgarh and Kohat, *Kazmi & Baquar Warsi s.n.* (PES); near Hangu towards Tal, *Kazmi 2641* (PES). KURRAM AGENCY: south of Parachinar, *Kazmi 2595* (PES). MALAKAND AGENCY: between Dargai and Malakand village, ca. 5 miles from Dargai, ca. 350 m., *Kazmi 370a* (PES); south of Malakand village, *Abid* in *Kazmi s.n.* (PES); 4 miles before Chakdara from Malakand, *Kazmi 2793* (PES). MIANWALI DIST.: Kalabagh, near bridge, *Kazmi s.n.* (PES). PESHAWAR DIST.: 7 miles from Peshawar towards Khyber Pass, near bridge, *Rodin 5276* (K, US); Islamia College, *Nath* in *R. R. Stewart 15803* (GH, MICH, US); Peshawar, *Nath 15419* (GH); ad radices boreales montium infra Cherat versus Pabbi, 500 m., *Rechinger 30263* (G, W); Peshawar to Cherat, *Lamond 1582* (E); Cherat, *Kazmi 2773* (PES); between Akora Khattak and Nowshehra, *Kazmi 2781* (PES); Khairabad, *Kazmi s.n.* (PES). QUETTA DIST.: Gumbaz, *Rechinger 29630* (G, W); Gumbaz to Barkhan, 100 m., *Lamond 1342* (E), *Kazmi 1804a* (PES); Quetta, *Lace 3683* (E). RAWALPINDI DIST.: Haroo, *Aitchison 1081* (K); between Texila and Rawalpindi, 5 miles from Texila, *Kazmi s.n.* (PES); 17 miles from Rawalpindi on Murree road, *Kazmi 2826* (PES); Islamabad, hills around Government offices, *Kazmi s.n.* (PES). WAZIRISTAN AGENCY: south Waziristan, Wana, 23.4.1939, *Ludlow 643* (E). ZHOB DIST.: 26 km. from Fort Sandeman on road to Wana, between Zhob and Sambaza, *Lamond 1442* (E), *Kazmi 1926a* (PES).

7. **A. guttata** Bunge, Index Sem. Horti Dorpat **1840**: 7. 1840; Ledeb. Fl. Rossica **3**: 139. 1847; I. M. Johnston, Jour. Arnold Arb. **33**: 331. 1952; M. Pop. Fl. URSS **19**: 176. 1953; Riedl in Rechinger, Fl. Iranica **48**: 157. 1967.

Arnebia tibetana Kurz, Jour. Asiat. Soc. Bengal **43**(2): 189. 1872; C. B. Clarke in Hook. Fl. Brit. India **4**: 176. 1883; M. Pop. Fl. URSS **19**: 177. 1953.
Lithospermum guttatum (Bunge) I. M. Johnston, Jour. Arnold Arb. **33**: 330. 1952, excl. *A. thomsoni* C. B. Clarke (1883), *in synon.*

TYPE: Hab. ad fluv. Ima in Tschiyam influentem [without citation of collectors name] *s.n.* (LE-holotype, P-isotype).

Erect, suberect to rarely decumbent or procumbent herb, flowering in the first year but becoming perennial, with dye-stained tap roots. Stems

usually many, simple or bearing short ascending branches, to 25 cm. long; densely to very densely covered with soft or stiff, spreading, white trichomes of various lengths, to 3 mm. long, arising from large, prominent, tuberculate bases. Basal leaves well developed, usually disappearing at anthesis, coriaceous, oblanceolate, entire, obtuse to roundish, attenuate towards the base, to 7 cm. long, 10 mm. broad, covered on both surfaces with trichomes, like those of the stem; cauline leaves oblong-ovate, shorter and narrower, usually more or less narrowed towards the base, rarely broad. Inflorescence of terminal cymes, at first glomerate, 1–2 cm. in diameter, elongating in age to 10 cm., bearing unilateral, closely set flowers; bracts usually equalling or slightly exceeding the calyx. Calyx erect, divided to the base, lobes linear, densely covered with trichomes to 1 mm. long, 7 mm. long in flower, elongated to 12 mm. in fruit. Corolla orange or yellow, minutely hairy with spreading or antrorsely subappressed trichomes externally, 14–19 mm. long, tube 10–15 mm. long with obvious suprabasal nectary of well developed villous collar, limb spreading, sometimes with a dark purple spot at each corolla sinus, 8–12 mm. in diameter. Flowers heterostyled. Stamens attached just above the middle of the corolla tube or near its summit and partially exserted; anthers 1.5–2 mm. long. Style reaching up to the middle of the tube or slightly exserted, usually distinctly forked with the branches once to several times as long as the stigma; stigmas two, reniform, entire or more or less bilobed. Nutlets dull gray or olivaceous, broadest at the base, ± tuberculate, attachment surface large, rough, usually with a quadrate prolongation upwards and outwards in the recessive angle beneath the base of the ventral keel of the nutlet, 2–3 mm. long.

DISTRIBUTION: Afghanistan, West Pakistan, Kashmir, northwestern India, Altai, Dsungaro-Tarbagatai, Tien Shan, Mongolia.

7a. Var. guttata.

Plants usually with many, much branched stems; calyx densely hairy, trichomes thin, soft, spreading; nutlets densely, minutely and usually uniformly tuberculate.

West Pakistan: CHITRAL STATE: Rosh Gol, northeast of Tirich Mir, 3000 m., *Stainton 2824* (BM); Trikho, 2600 m., *Bowes Lyon 1036* (BM). GILGIT AGENCY: Baltistan, above the Indus River, near Skardu, 2300 m., *Webster & Nasir 5763* (GH, RAW); Skardu, 7500 m., *Siddiqui, Nasir & Zaffar 4233* (BM); Skardu, 2400 m., Aug. 4, 1876, *C. B. Clarke 30037A* (K), *30037* (BM), 2200–2500 m., *Duthie 12064* (BM, E), 2500 m., *R. R. Stewart 20392* (US); Bar Loongma Nullah, Mount Haramah, 2200 m., *Ludlow 261* (BM); Tsumgak, on the northern foot of the Tsorbat La Pass, to Poen, opposite Tsorbat, *Schlagintweit 6060* (GH); on the right side of the Shayok, via Kiris to Neru, on right side of Indus, *Schlagintweit 5811* (BM, GH); Kris to Parkutta, Indus Valley, 2500 m., *R. R. Stewart 20924* (GH); Udmaro, 3000 m., *Koelz 9626* (GH); Kardong to Diskit, on the left side of Shayok, *Schlagintweit 2273* (US); Shayok Valley, Doghari to Kuru, 2700 m., *R. R. Stewart 20853* (GH); Hispar Valley, 2700–3000 m., *Russell 1178* (BM), 2700 m., *Russell 1843* (BM); above Nomal, 1700 m., *R. R. Stewart 26325* (BM),

July 17, 1954, *R. R. Stewart s.n.* (MICH); entre Astor et Bunji, 1300–2300 m., *Schmid 1809* (BM), *Schmid s.n.* (MICH); Karakoram, Sassir Pass, 3500 m., July 1925, *Meinertzhagen 53* (BM), *s.n.* (BM). Miscellaneous: Tibet occ., regio alp., 14000–16000 ped., Herb. Ind. Orient. Hook. f. & Thoms., *Thomson, s.n.* sub *Arnebia* No. 7 (GH, BM).

Kashmir: Leh, Hemis nullah, 4500 m., *Ludlow & Sherriff 8470* (BM); Ranbirpur, Indus Valley, 3000 m., *Ludlow & Sherriff 8482* (BM, GH); Pitug, *Koelz 6517* (GH, MICH, US); Nima Mud, 3500 m., *Koelz 3333a* (E, GH, US); Chakar Talao, 3000 m., *Koelz 2459a* (GH); Hemis, *Koelz 6391* (MICH); Kugzil La, Rupshu, 5000 m., *Koelz 2325* (GH), 4000 m., *Koelz 2323a* (GH, US); near Kyber, April 1915, *Mrs. Prescott-Decie, s.n.* (BM); Indus *Valley, near Pituk*, 3100 m., *Voigt 1060* (US).

7b. Var. **thomsonii** (C. B. Clarke) Kazmi, comb. nov.

Arnebia thomsonii C. B. Clarke in Hook. f. Fl. Brit. India **4**: 176. 1883; M. Pop. Fl. URSS **19**: 177. 1953.

TYPE: Tibet occ., regio alp., 14,000 ped., Herb. Ind. Or. Hook. f. & T. Thoms., *T. Thomson, s.n.* as *Arnebia* No. 6 (K-holotype, GH-isotype).

Plants usually with single or poorly branched stems; calyx very densely hairy, trichomes thick, stiff, subappressed; nutlets smooth or sometimes with few scattered tubercles.

West Pakistan: GILGIT AGENCY: Baltistan, Piti Valley, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH, K).

Kashmir: Reported from Ladak, Leh, *Lance s.n.* (K?).

The widely distributed species, *Arnebia guttata*, is very variable in the form of its leaves and in the type of trichomes they bear. In variety *guttata* many spreading or decumbent stems which are usually profusely and subdivaricately branched arise from the root. The cauline leaves vary from linear (*Stewart 26325*) to broadly lanceolate (*Mrs. Prescott-Decie s.n.*). The upper part of the stem, inflorescence, and the calyces are densely covered, usually with long, thin spreading trichomes. The nutlets are uniformly tuberculate, at least on their dorsal surface. Var. *thomsonii* differs from the typical variety in having an erect, single stem, which is hardly branched. Leaves and calyces are very densely covered with trichomes, which are much longer, thicker, and pungent compared to those of var. *guttata*. The sepals are more or less completely covered with such trichomes. The bracts in var. *thomsonii* are also comparatively broader than those of the typical variety. All these characters correlate well with the nutlets, smooth or with few scattered tubercles on the dorsal surface. C. B. Clarke (*l. c.*) gave some differences in measurements of the nutlets and of the corolla tube, which I was able to verify. M. Popov (*l. c.*) differentiated *Arnebia tibetica* from *A. guttata* but I did not find sufficient difference between the two to justify their separate identity.

8. **A. fimbriopetala** Stocks, Hook. Jour. Bot. & Kew Gard. Misc. **3**: 180. 1851; Boiss. Fl. Orient. **4**: 205. 1875; Riedl in Rechinger, Fl. Iranica **48**: 157. 1967.

Arnebia bungei Boiss. Fl. Orient. **4**: 215. 1875.
Echioides bungei (Boiss.) Rothm. Repert. Sp. Nov. **49**: 56. 1940.
Lithospermum fimbriopetalum (Stocks) I. M. Johnston, Jour. Arnold Arb. **33**: 326. 1952.
Lithospermum bungei (Boiss.) I. M. Johnston, *ibid.*
Arnebia fimbriopetala var. *bungei* (Boiss.) Riedl in Rechinger, Fl. Iranica **48**: 157. 1967, *syn. nov.*

TYPE: Upper Baluchistan, *Stocks 977* (K-holotype).

ICON.: Stocks, l. c. **3**: 180. *t. VI.* 1851.

Erect to suberect annual herb with short dye-stained tap roots. Stems usually solitary or rarely few, slender, sparingly branched near the base, branches spreading, 5–15 cm. long, covered with soft, crisped, white, usually antrorsely appressed to subappressed, trichomes without tuberculate bases. Basal leaves few, oblong-ovate, entire, sometimes irregularly revolute, with roundish apex, slightly narrowed towards the base, thick, 20–25 mm. long, 5 mm. broad; both surfaces covered ± uniformly, with very short, very thin, subappressed trichomes to 0.5 mm. long, arising from prominent tuberculate bases, rarely glabrous below; cauline leaves few, sessile, shorter and narrower, sometimes ciliate on the margins of the lower half. Inflorescence simple or geminate, with closely set flowers, bracteate, bracts leaflike, sometimes ciliate at the margins, to 6 mm. long, 1.5 mm. broad at base. Pedicels stout, ± 1 mm. long. Calyx divided nearly to the base, lobes linear, obtuse, bearing minute trichomes on both surfaces and densely so on margins, 15–17 mm. long, 1.5 mm. broad at base in flower, enlarged at maturity, glabrescent with midrib becoming prominent, erect, to 30 mm. long, with major lobes 3–5 mm. broad near the base, in fruit. Corolla yellow, externally villulose, 25–30 mm. long, tube slender, surpassing the calyx, 20–24 mm. long, bearing a membranous more or less hairy collar-like nectary inside above the base, 0.5–1 mm. high, throat without glands or appendages, limb 10–20 mm. in diameter, lobes broad, rounded, with distinctly lobulate or fimbriate margins. Flowers heterostyled, in long-styled flowers the corolla tube cylindrical, abruptly enlarged below the summit, 6–8 mm. in diameter. Anthers 2–2.3 mm. long, attached low in the upper third of the corolla tube; filaments short. Style slender, forked at apex, lobes 0.5 mm. long; stigmas 2, compressed, as broad as long, obscurely bilobed. In short styled flowers corolla tube gradually ampliate, anthers attached at the summit of the corolla tube with their upper third exserted; style two-thirds as long as the corolla tube. Nutlets olive-green to reddish, beaked above the middle, lower half of dorsum swollen on either side of a broad depression, upper half with a low rounded medial keel, venter angulate, attachment surface broadly triangular, basal, gynobase very depressed, 3–3.5 mm. long, 3 mm. broad at the base.

DISTRIBUTION: Iran, Afghanistan, West Pakistan.

West Pakistan: MAKRAN DIST.: Between Pasni and Kappar, road to Gwader, *Kazmi 1011* (PES); *Lamond 456* (E), *Rechinger 27871* (G, W). QUETTA DIST.:

Doband, Chiltan, *Stocks s.n.* (K); Gwal, *Munro s.n.* (K); Maslakh. *R. R. Stewart 28281* (K, RAW); Chahar Sar, *Crookshank 69* (K).

Riedl (*l. c.*) distinguished *Arnebia fimbriopetala* var. *bungei* from the typical variety, by attributing to var. *bungei* the crenate or subentire corolla lobes and to var. *fimbriopetala* deeply fimbriate corolla lobes. Variety *bungei* is based on Bunge's collection (Ssertschah, 12 Mart., 1859; c-holotype, GH-isotype) from Persia. A careful study of this collection and other material from the area showed that the depth of laceration of the corolla lobes varies from plant to plant and this character can not be correlated with any other. Therefore, I came to the conclusion that *A. fimbriopetala* and *A. bungei* are conspecific.

9. **A. linearifolia** A. DC. in DC. Prodr. **10**: 95. 1846; Boiss. Fl. Orient. **4**: 214. 1875; M. Pop. Fl. URSS **19**: 182. 1953; Riedl in Rechinger, Fl. Iranica **48**: 162. 1967.

Arnebia flavescens Boiss. Diagn. Pl. Orient. **11**: 117. 1849.
Echioides linearifolium (A. DC.) Rothm. Repert. Sp. Nov. **49**: 56. 1940.
Lithospermum aucheri I. M. Johnston, Jour. Arnold Arb. **33**: 328. 1952.

TYPE: In deserto Syriaco, *Aucher-Eloy 2368* (G-holotype).

Erect to suberect annual herb with tap root and lower part of stem dye-stained. Stems usually many, spreading, sparingly branched, to 15 cm. long; stem and branches rarely totally glabrous, sometimes partly subglabrous, but usually covered sparsely to densely with thin white, antrorsely subappressed or spreading very short trichomes, to 1 mm. long, usually not at all to sometimes with tuberculate bases, intermixed with few scattered, stout spreading trichomes, to 2.5 mm. long, arising from prominent large tuberculate bases. Basal leaves few, disappearing at anthesis, oblong, entire, with roundish or subobtuse apex, attenuated towards the base, sometimes into short petioles, to 5 cm. long, 3–10 mm. broad, upper surface densely, lower surface sparsely covered with short subappressed trichomes, or the lower surface sometimes subglabrous; sometimes the lower half of the leaves with long trichomes on the margins; cauline leaves few, subsessile, obtuse to subacute with more long trichomes tuberculate at the base on both surfaces and margins. Inflorescence short, compact in flower, later elongated, to 12 cm. long, bracteate, bracts leaflike, shorter and narrower. Pedicel very short in flower, stout, hairy and elongated to 3 mm. in fruit. Calyx divided most of its length, lobes erect, linear, obtuse, densely covered with short trichomes, intermixed with long trichomes usually near the base, without prominent nerves, 6–10 mm. long, 1–1.5 mm. broad at the base in flower, much enlarged, lobes free 2.5–3.5 mm. above the base of the calyx, much dilated at the base in fruit, with very stout and hardened midrib and prominent veins in the lower parts, midrib and the margins bearing very long, stiff, white trichomes, arising from large mamilliform tubercles, to 22 mm. long, 3–5 mm. broad at base. Corolla yellow, subtubular, densely hairy externally, 10–14 mm.

long, tube slender, usually surpassing the calyx by 2–3 mm., nectary a papery lobulate collar, ca. 0.5 mm. high, throat glabrous, without glands or appendages, limb of small ascending lobes, to 4 mm. in diameter. Anthers attached at the summit of the corolla tube, included. Style reaching 1–3 mm. below the anthers, short, forked at apex, bearing 2 compressed, reniform stigmas. Nutlets rubiginous, sparingly punctate and tuberculate to sometimes rugose, back rounded, 2.5–3 mm. long, ca. 2 mm. broad near the base.

DISTRIBUTION: North Africa, Transcaucasus, Syria, Iraq, Iran, Afghanistan, West Pakistan.

West Pakistan: KALAT DIST.: Between Kalat and Mastung, 1800 m., *Jafri & Akbar 2001* (E). MAKRAN DIST.: Between Hushab and Panjgur, 20–30 km. from Panjgur, *Kazmi 1186b* (PES), *Lamond 566* (E), *Rechinger 28150* (W); about 10 miles from Hushab towards Panjgur, *Kazmi 1159b* (PES). QUETTA DIST.: Pishin, 29.3.1889, *Lace*, Herb. Watt No. *3566* (E); Quetta below Yaro and Sarnan, 6 miles from Quetta, on Quetta-Chaman Road, *Kazmi 1497* (PES); Quetta to Chaman, Yaro near Bostan, ca. 40 km., from Quetta, 1450 m., *Lamond 587* (E), *Kazmi 1480b* (PES), *Rechinger 28927* (G, W). Reported from Qilla Abdullah, *Duthie 8681*; 45 km. east Mirjaveh, 800 m., *Grant 15329*; Baluchistan, without locality, *Stocks s.n.* (?).

Riedl (*l. c.*) differentiated *Arnebia linearifolia* into two subspecies, viz. subsp. *linearifolia* and subsp. *desertorum* Riedl (Oesterr. Bot. Zeitschr. **109**: 74. 1962). Subsp. *desertorum* is distinguished from our subspecies by having much dilated bases of the calyx lobes at fruiting stage, which are to 10 mm. broad. Subspecies *desertorum* is confined to Iraq, whereas the typical subspecies is distributed all over the area cited for the species.

10. **A. decumbens** (Vent.) Coss. & Kral. Bull. Soc. Bot. France **4**: 402. 1857; M. Pop. Fl. URSS **19**: 180. 1953; Riedl in Rechinger, Fl. Iranica **48**: 159. 1967.

Lithospermum decumbens Vent. Descr. Pl. Jard. Cels. 37. 1801.
Lithospermum micranthum Viv. Fl. Lib. Spec. 10. 1824.
Onosma divaricatum Lehm. Asperif. 372. 1818.
Lithospermum cornutum Ledeb. Fl. Alt. **1**: 175. 1829.
Arnebia cornuta (Ledeb.) Fisch. & C. A. Mey. Index Sem. Hort. Petrop. **1**: 22. 1835.
Arnebia vivianii Coss. & Dur. Ann. Sci. Nat. Ser. 4. **1**: 240. 1854.
Arnebia orientalis Lipsky, Acta Horti Petrop. **26**: 513. 1910.

TYPE: Inter Baghdad et Hit, *Bruguiere & Olivier s.n.* (P-holotype).

Annual suberect herb with slender, dye-stained tap roots. Stems pale, usually many, branched near the base, to 30 cm. long, covered densely with white, soft, subappressed trichomes, to 0.5 mm. long, intermixed with long, stiff, spreading trichomes, to 2–2.5 mm. long, long trichomes with distinctly, and short ones without or with only inconspicuous tuberculate bases. Basal leaves usually disappearing at anthesis, oblong-ovate, entire,

sometimes revolute at the margins, with roundish apex, gradually attenuated towards the base, 2–3 cm. long, 2–5 mm. broad, covered on both surfaces with short and long trichomes, to 1 mm. long, usually longer towards the base of the leaves, nerves sunken above, prominent below; cauline leaves sessile, oblong to oblong-lanceolate, usually broadest at the middle of the lower half, entire, slightly revolute in the upper half, obtuse, to 2.5 cm. long, 5 mm. broad, lower surface sometimes subglabrous, but usually bearing shorter trichomes on both surfaces. Inflorescence terminal, simple to geminate, short and congested in flower, later elongated to 9 cm., bearing fruits to 10 mm. distant, bracteate, bracts leaflike, usually bearing some long trichomes on the margins and midrib of their lower half, flowers sessile, fruits subsessile. Calyx divided nearly to the base, lobes linear much shorter than the corolla tube, 4–5 mm. long, ca. 0.5 mm. broad in flower; fruiting calyx 10–15 mm. long, connate 2–3 mm. from the base, lobes linear in the upper half, much dilated below, midrib stout, hardened, subconnate to connate, lateral veins reticulate and very prominent in the connate part, bearing few to many stiff, white trichomes usually with tuberculate bases, lobes 7–12 mm. long, 1.5 mm. broad at base. Corolla yellow, tubular-infundibuliform, densely pubescent externally, especially on the lobes, to 12 mm. long, tube slender, widened gradually from the middle upwards, throat ca. 1–5 mm. wide, limb ascending, lobes roundish, ca. 1 mm. long and broad. Anthers attached above the middle or on the throat of the corolla tube, ca. 0.8 mm. long, filaments very short. Style reaching the middle of the upper half of the corolla tube, bifid to once again bifid, stigmas 4, capitate. Nutlets brown, beaked, ventrally and supradorsally keeled, dorsally densely tuberculate, 2–2.5 mm. long, 1–1.5 mm. broad at the base.

DISTRIBUTION: North Africa, Syria, Caucasus, Iraq, Iran, Afghanistan, West Pakistan, Turkestan, Pamir Alaj, Tien Shan, China.

West Pakistan: KALAT DIST.: Punjgur to Surab, Basima near Jangal, 1350 m., *Lamond 662* (E), *Kazmi 1263* (PES); between Kolpur and Machh, *Kazmi 1333b* (PES); near Nag, *Kazmi 1249b* (PES). QUETTA DIST.: between Qilla Abdullah and Sheila Bagh, *Kazmi 1520* (PES); Quetta to Chaman, Yaro near Bostan, ca. 40 km. from Quetta, 1450 m., *Lamond 991* (E); Yaro prope Bostan, 40 km. NNE Quetta versus Pishin, 1450 m., *Rechinger 28928* (G, W); ad radices occidentales montium Chiltan, inter Dulai et Kanak, 1600 m., *Rechinger 29144* (G, W); on way to Ziarat from Quetta, 2170 m., *Jafri & Akbar 2025* (BM, E); Spin Karez, hills on the side of water reservoir, *Kazmi 1583a* (PES); Sultan, Maslakh Range, *R. R. Stewart 29292* (MICH); Quetta, *Crookshank 11* (K); Pishini Forest Nursery, *Kazmi 1421b* (PES). Reported from Khuzdar, *Rechinger 27400* (W); Makran 20–30 km. S. Punjgur, *Rechinger 28131* (W); between Raghoi and Sishk, *Hotson s.n.*; Kharan, *Hughes-Buller 23184, 23148*; *Stocks s.n.*

Arnebia decumbens is separated by Riedl (*l. c.* **48**: 160. 1967) into subsp. *decumbens* and subsp. *macrocalyx*. Subspecies *macrocalyx* (Coss. & Kral.) Riedl is based on *Arnebia decumbens* var. *macrocalyx* Coss. & Kral. (Bull. Soc. Bot. France **4**: 403. 1857) and is distinguished from the

typical subspecies by having fruiting calyx lobes dilated to 1.5 mm., and the lower connate part covered with white tubercles; it is confined to North Africa and southern Iran, whereas the typical subspecies is distributed in our area and is spread over the area of distribution of the whole species.

11. **A. grandiflora** (Trautv.) M. Pop. in Lapin. Opred, rast. Taschkentsk. Oasisa 342, No. 319. 1938, Fl. URSS. **19**: 705. 1953; Riedl in Rechinger, Fl. Iranica **48**: 161. 1967.

Arnebia cornuta (Ledeb.) Fisch. & C. A. Mey., var. *grandiflora* Trautv. Bull. Soc. Nat. Mosc. **4**: 422. 1866.
Arnebia orientalis Lipsky, Acta Horti Petrop. **26**: 522. 1910.

TYPE: Ad urbem Tashkent pagum Toj-Tjube, inter Tashkent et Angren, *Regel s.n.* (LE-holotype).

ICON.: Riedl, l. c. *t. 47. fig.* 1967.

Annual erect or suberect herb with slender, dye-stained tap roots. Stems simple or branched, branches divaricate (at least in specimens from West Pakistan), to 50 cm. long; stem and branches densely covered with short, crisped, white, subappressed to suberect trichomes, to 0.5 mm. long, intermixed profusely with long, stiff, pungent, spreading trichomes, to 2 mm. long, arising from prominent tuberculate bases. Basal leaves oblong to oblong-lanceolate, entire, with roundish to subobtuse apex, narrowed gradually towards a broad base, to 5 cm. long and 6 mm. broad, covered on both surfaces with slender, crisped, spreading trichomes, on the upper surface arising from very prominent tuberculate bases, to 0.5 mm. in diameter, on the lower surface from smaller tubercles, intermixed with minute trichomes, to 0.5 mm. long; middle cauline leaves 60–70 mm. long and 8 mm. broad; upper cauline leaves gradually reduced in size upwards. Inflorescence short and congested in flower, later elongated to 12 cm.; bracts densely hairy, linear-lanceolate, acute, usually shorter than the calyx. Pedicel lacking in flower, developed but short in fruit. Calyx divided nearly to the base, lobes linear-filiform in flower, 5–6 mm. long, to 0.5 mm. broad at base, hairy, erect, lobes elongated to 15 mm. connate and dilated at base, to 1 mm. broad in fruit, covered densely with short, subappressed trichomes without basal tubercles, intermixed with some erect, long, pungent, stiff trichomes with large tuberculate bases. Corolla yellow with prominent large dark patches at the corolla lobes, minutely hairy externally, 20–35 mm. long, tube narrow, slender, to 18 mm. long, then gradually widened into a funnelformed throat, to 6 mm. long, limb to 6 mm. long and 15 mm. in diameter, lobes roundish, entire, spreading. Flowers heterostyled. Anthers attached in the throat at equal or different levels; filaments short. Style reaching the middle of the corolla tube or its throat, sometimes exserted, slender at apex, bifurcate, branches short; stigmas 4, ± clavate. Nutlets dark greenish-brown, pyramidal, subcordate at base, abruptly narrowed at the middle into a triangular

upper part, to 1 mm. long, ventrally and supradorsally slightly keeled, unequally tuberculate all over the surface, ca. 2 mm. long and broad at base.

DISTRIBUTION: Iran, Afghanistan, Turkestan, West Pakistan.

West Pakistan: CHITRAL STATE: Mastuj, 1950 m., *Stainton 2463* (BM). ZHOB DIST.: between Zhob and Sambaza, 15–16 miles on Fort Sandeman-Wana Road, *Kazmi 1908* (GH, PES), *Rechinger 29837* (G, W).

The material collected from Chitral agrees in all details with the type and other material collected from Turkestan and Afghanistan. The specimens (*Kazmi 1908*, *Rechinger 29837*) collected from north Baluchistan differ from the type material in being more profusely branched with the inflorescence composed of many closely set flowers or fruiting calyces. The calyx lobes are not at all connate at base in fruit; are more densely pubescent with trichomes slender and long. The flowers are usually longer than in the plants from Turkestan. I could not examine any material from Iran and, of course, not much even from West Pakistan to establish this variation fully. On further study, with more material in hand, the plants from Baluchistan may prove to be a subspecies or even a distinct species worthy of recognition.

12. **A. waziristanica** H. Riedl, Oesterr. Bot. Zeitschr. **109**: 58. 1962; in Køie & Rechinger, Biol. Skr. 13(4): 245. 1963, in Rechinger, Fl. Iranica **48**: 156. 1967.

TYPE: PAKISTAN: Waziristan, 21 May 1895, *Harsukh 15803* (DD-holotype).

ICON.: Riedl, l. c. *fig. 193*. 1963.

Annual herb. Stems branched at the base, branches numerous, procumbent to ascendent, 15–20 cm. long, covered with soft trichomes equalling the diameter of the stem in length. Leaves scanty, narrow-lanceolate, to 5 cm. long, 4–6 mm. broad, covered sparsely on both surfaces with trichomes arising from tuberculate bases. Inflorescence elongate, simple to divided at base, 3–20 cm. long; bracts slightly shorter than the calyx, narrow-linear, similar to the calyx lobes. Calyx short pedicellate, divided nearly to the base, densely covered in the lower parts with long, white, spreading trichomes, lobes narrowly linear, subfiliform, 7–10 mm. long in flower, to 15 mm. long, 1 mm. broad in fruit. Corolla scarcely exceeding the calyx, in dried specimens brown to dark purple, infundibuliform, externally pilose, tube slender, hardly 1 mm. in diameter, widened upwards to 2 mm., annulate within at the base. Flowers distinctly heterostyled. Anthers sessile, attached at the base of the limb or above the middle of corolla tube at the same level. Style in long-styled flowers 9–10 mm. long; stigmas 2, minute, capitate; not seen in short-styled flowers. Nutlets ventrally distinctly keeled, densely minutely verruculose and indistinctly rugulose, 2–3 mm. long.

DISTRIBUTION: West Pakistan.

West Pakistan: Waziristan, *Harsukh 15803* (DD).

I could not examine any plant of this taxon. The description given is according to Riedl (*l. c.*). From the description *Arnebia waziristanica* appears to be closely related to *A. griffithii* and *A. hispidissima*, from which it is distinguished by its brown to dark purple flowers.

13. **A. simulatrix** H. Riedl, Oesterr. Bot. Zeitschr. 109: 70. 1962, in Køie & Rechinger, Biol. Skr. 13(4): 243. 1963.

TYPE: Afghanistan, *Neubauer 205* (w-holotype).

ICON.: Riedl, l. c. *fig. 3*. 1962; l. c. *fig. 192*. 1963.

Annual herb with an elongate, fusiform dye-stained root. Stems simple to branched, to 10 cm. long, covered with stiff trichomes. Basal leaves disappearing at anthesis; cauline leaves few, lanceolate, to 6 cm. long and 6 mm. broad, densely covered on upper surface, margins, and midrib, loosely so on the lower surface, with stiff, spreading to subappressed trichomes. Inflorescence short, congested in flower, 1–2 cm. long, later elongated to 4–5 cm.; bracts lanceolate, shorter than the calyx, dilated at base. Pedicels hardly developed in flower, to 2 mm. long in fruit. Calyx 8–12 mm. long in flower, 18–20 mm. long in fruit, connate from the base up for 3 mm., scarcely angulate, medial nerve less prominent compared to that in *Arnebia decumbens* (Vent.) Coss. & Kral., bearing some long tricomes, arising from minute tuberculate bases, which are gradually reduced in size upward; lobes pilose externally and at the midrib, 1 mm. broad in flower, 2–3 mm. broad in fruit. Corolla yellow, densely pilose externally, infundibuliform, 15–18 mm. long, tube thick, dilated at the throat, 2–2.5 mm. in diameter, glabrous internally, lobes erect to slightly recurved, margins ciliate, to 1 mm. long. Anthers 5, three attached 3 mm. below, and the other two ca. 5 mm. below the margins of the corolla lobes. Style 10–12 mm. long, bifid to once branched; stigmas 4. Nutlets 4, sessile, horizontal, acuminately beaked, dorsally convex, slightly keeled in the upper part, verruculose, ventrally angulate, obtusely keeled, the two faces minutely verruculose, 3–3.5 mm. long.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: QUETTA DIST.: 8 km. northwest of Harnai, 1000 m., *Rechinger 29551* (w).

In habit *Arnebia simulatrix* is very similar to *A. linearifolia*, from which it is distinguished by having 4 distinct stigmas. It is also closely related to *A. decumbens* but differs from that species by its less dilated calyx lobes and less prominent midrib on the connate part of the calyx in fruit.

29. **Onosma** L. Sp. Pl. ed. 2. 1: 196. 1762; Gen. Pl. ed. 6. 76. 1764.

TYPE SPECIES: *O. echioides* L.

Perennial or biennial, coarsely hispid, herbs or sometimes undershrubs. Leaves various, usually numerous. Inflorescence of single or of paired terminal cymes, usually not much elongated in fruit, bracteate. Flowers regular and radially symmetrical. Calyx usually accrescent and divided to the base or sometimes with a short tube, lobes 5, equal, linear lanceolate, oblanceolate, or ligulate. Corolla yellow, blue or rarely white or red, tubular, obconic-tubular or rarely ellipsoid, usually gradually broadening upwards from the base; inside the base of the tube a well developed nectariferous ring or collar, the throat without faucal appendages, lobes small erect or with tips more or less recurved. Anthers elongate, terminated by well developed appendages, usually coherent at the base or frequently joined laterally by the interlocking of minute marginal trichomes to form a tube, terminal appendages elongate, usually hyaline and chartaceous, tips emarginate, basal appendages usually short and thick, filaments inserted below, near, or above the middle of the corolla tube, short to very long Stigmas 2. Nutlets 4, erect, venter usually angled, dorsum convex or sometimes flattened below the middle, attachment scar basal, usually triangular, as broad as long, horizontal or somewhat oblique. Gynobase pyramidal or flat or even depressed at the center, the attachment faces usually distinct, frequently concave.

Species about 85, with greatest diversity and maximum concentration in Iran, distributed westward to Syria and Turkey, eastward and northeastward to Turkestan, Altai, China, Afghanistan, West Pakistan, Kashmir, Tibet, and India to Burma.

Key to the Species

a. Anthers united only at the base, laterally free.
  b. Corolla shorter than, or at most equalling the calyx; bracts lanceolate with excessively prolonged tips; leaves densely clothed with minute, pallid trichomes on the lower surface. ..... 7. *O. bracteatum.*
  b. Corolla longer than the calyx, obviously surpassing the calyx lobes; bracts lanceolate or subulate with acute tips; lower surface variously pubescent.
    c. Corolla 25–40 mm. long; anthers 9–12 mm. long; filaments 3–5 mm. long; nectary glabrous; nutlets 4–5 mm. long. 8. *O. dichroanthum.*
    c. Corolla 8–15 mm. long; anthers 4–6.5 mm. long; filaments 2–2.5 mm. long; nectary pubescent; nutlets 3–4 mm. long. 9. *O. limitaneum.*

a. Anthers united laterally as well as basally, forming a tube.
  d. Anthers more than half to completely exserted from the corolla.
    e. Base of filaments and adjacent corolla tube villous; corolla externally covered with antrorsely appressed trichomes; trichomes on the lower surface of the leaves appressed. ..... 5. *O. hypoleucum.*
    e. Base of filaments and adjacent area glabrous; corolla externally covered with retrorsely appressed trichomes, trichomes on the lower surface of the leaves spreading. ..... 6. *O. thomsonii.*
  d. Anthers included in the corolla or with only their tips exserted.
    f. Filaments 2–2.5 mm. long, base of the anthers about opposite the base of filaments. ..... 1. *O. chitralicum.*

f. Filaments 5–10 mm. long, base of the anthers 2–6 mm. above the base of the filaments.
  g. Plants with strong perennial root; stems 10–75 cm. tall; basal leaves 10–40 cm. long, 5–15 mm. broad. ..... 2. *O. hispidum.*
  g. Plants with biennial or short-lived roots; stems 10–30 cm. tall; basal leaves 4–10 cm. long.
    h. Bracts of the inflorescence with slenderly attenuate upper part and acuminate tips; corolla 30–32 mm. long; filaments 9–10 mm. long. ..... 3. *O. khyberianum.*
    h. Bracts of inflorescence not slenderly attenuate in the upper part, tips acute; corolla 22–30 mm. long; filaments 6–9 mm. long. ..... 4. *O. griffithii.*

1. **O. chitralicum** I. M. Johnston, Jour. Arnold Arb. **32**: 209. 1951; Riedl in Rechinger, Fl. Iranica **48**: 179. 1967.

TYPE: WEST PAKISTAN: Chitral, *S. M. Toppin 48* (K-holotype).

Perennial herb with a stout woody root. Stems many, erect or ascending, branched above, to 30 cm. long, 7 mm. thick at the woody base; densely covered with minute, thin, spreading trichomes, to 0.2 mm. long, intermixed sparsely to profusely with long, pungent trichomes, to 4 mm. long, arising from prominent, white, tuberculate bases, ± retrorsely subappressed on the lower parts of the stem, spreading on the upper parts. Basal leaves persistent at anthesis, oblong-spathulate, entire, sometimes revolute at the margins, roundish to subobtuse, elongate and gradually narrowed towards the base, to 6 cm. long and 8 mm. broad, nerves on the upper surface sunken, raised below, both surfaces densely puberulous or hispidulous, also uniformly covered on the upper surface with long, white, slender, erect, unequal trichomes, to 3 mm. long, with tuberculate bases, such trichomes comparatively denser on the margins and the midrib; middle cauline leaves narrowly oblong to spathulate, roundish to subobtuse, to 10 cm. long and 14 mm. broad; upper cauline leaves broadly lanceolate, subobtuse to acute, roundish at base, to 8 cm. long and 15 mm. broad. Inflorescence scorpioid, short in flower, later elongate, forked, branches to 13 cm. long, bracteate, bracts sessile, leaflike, shorter and narrower, acute, slightly dilated at base. Pedicels in flower 3–5 mm. long, slender, elongated to 8 cm. in fruit. Calyx hairy, divided to the base, lobes narrowly lanceolate, 8–10 mm. long, 1–1.5 mm. broad in flower, enlarged to 10–12 mm. long and 2 mm. broad in fruit. Corolla white, brownish in dried state, cylindrical-campanulate, externally subglabrous to minutely puberulous, glabrous within, 12–14 mm. long, tube 2.5 mm. thick at base, gradually widened upwards, lobes short, at the base with a glabrous nectary, 0.2–0.3 mm. high. Anthers united laterally as well as basally, forming a tube, slightly exserted, 6–7 mm. long; filaments linear, inserted below the middle of the corolla tube, 2–2.5 mm. long. Style ca. 15 mm. long, slightly exserted from the corolla, stigma not conspicuous. Nutlets 3–4 mm. long, smooth, shining.

DISTRIBUTION: West Pakistan.

West Pakistan: CHITRAL STATE: Chitral, *Toppin 481* (K-type); Chitral village, 10 miles south, 1350 m., *Stainton 2216* (BM).

Onosma chitralicum is based on the collection of Toppin from Chitral. In the type specimen the basal parts of the plant are missing. I. M. Johnston, in his description, assumed this plant to be an annual. On close examination of another specimen collected from the same locality by Stainton, which is very complete in all respects, the species proves to be a perennial. It has a strong, thick woody root and persistent basal leaves. The description of the basal parts of the plant, therefore, has been completed above.

Riedl (l. c. **48**: 185. 1967) cited the collection (*Stainton 2216*) under *Onosma limitaneum* subsp. *limitaneum*, and probably his measurements of the leaves of subsp. *limitaneum* are also based on this plant.

Onosma chitralicum is distinguished from all related species in our area by having laterally as well as basally united, very short anthers, filaments 2–2.5 mm. long, with the bases opposite the bases of anthers, and white corollas.

2. **Onosma hispidum** Wall. ex G. Don, Gen. Syst. **4**: 317. 1838; Riedl in Rechinger, Fl. Iranica **48**: 177. 1967.

Onosma hispida Wall. Cat. No. 938. 1829, *nomen nudum*.
Onosma kashmiricum I. M. Johnston, Jour. Arnold Arb. **21**: 50. 1940.
Onosma hispidum var. *kashmiricum* (I. M. Johnston) I. M. Johnston, Jour. Arnold Arb. **32**: 210. 1951.

TYPE: INDIA: Kumaon, *Wallich 938* (K).

Perennial herb with a strong, thick, tap root. Stems fistulous, usually many, simple or rarely branched, 10–70 cm. long, 3–6 mm. thick at base, covered densely with bristly, spreading white trichomes, to 4(–5) mm. long, arising from large tuberculate bases, the area between the bases, sometimes quite glabrous, densely puberulous, or bearing very short, spreading trichomes. Basal leaves persisting at anthesis, narrowly oblanceolate, entire, roundish, obtuse or at times subacute, usually attenuate towards the base, midrib inconspicuous above, raised and prominent below, indument similar to that on the stems, trichomes on the upper surface ± subappressed, spreading below; middle cauline leaves sessile, linear to lanceolate-oblong, obtusish, 4–10 cm. long, 4–10 mm. broad; upper cauline leaves, shorter, narrower to sometimes comparatively broader. Inflorescence of terminal, geminate cymes, dense at flowering, 3–4 cm. in diameter, racemose, elongating to 15 cm. long in fruit; bracts lanceolate, broad at base, gradually narrowed towards the acute apex. Pedicels hairy, 1–3 mm. long in flower, 5–10 mm. in fruit. Calyx divided to the base, lobes lanceolate, acute, covered with ± subappressed trichomes like those of the leaves, 12–15 mm. long in flower, 15–25 mm. long in fruit. Corolla white, cream to pale yellow, externally sparsely hispidulous, puberulous on lobes, glabrous

inside, 18–30 mm. long, 3–3.5 mm. thick at base, expanding gradually upwards, 8–11 mm. wide just below the sinuses, lobes 1.5 mm. high, recurved outside. Anthers united basally and laterally to form a tube, 9–11 mm. long, tips 2 mm. long; filaments ligulate 5–9 mm. long, decurrent bases to 5 mm. long, inserted 8–13 mm. above the corolla base. Nectary glabrous, collar ± 0.3 mm. high. Style glabrous, 13–23 mm. long. Nutlets ± 6 mm. long, smooth, obscurely roughened, ± shining.

DISTRIBUTION: Afghanistan, West Pakistan, Kashmir, northwestern India.

West Pakistan: CHITRAL STATE: Kafiristan, Rumbur-Gangalwat Gol, 2850 m., *Bowes Lyon 669* (BM); Basin Gol, 3450 m., *Bowes Lyon 952* (BM); Chitral village, 1500 m., *Stainton 2182* (BM). GILGIT AGENCY: Naltar, 3500 m., *R. R. Stewart 26341* (BM); Astore, Gudhai Valley, 3500–3900 m., July 21, 1892, *Duthie s.n.* (BM); Kamri Kotal, 3600 m., *Giles 140* (K); expedition to Karakoram Glacier, 1892, *Conway 335* (K). HAZARA DIST.: Kaghan Valley, Naran, *Anwar Ali 117* (MICH); Naran to Saiful Maluk Sar, 2900 m., *Kazmi 2273a* (PES); Naran, near the top of Ganji Pahari, 2950 m., *Kazmi 369a* (PES); Batakundi, near Rest House, 3000 m., *Kazmi 408b* (PES); between Batakundi and Burawai, *Burtt & Arshad 920* (E); Shogran to Makara, 3000 m., *Kazmi 446b* (PES); Besar, June 22, 1899, *Inayat s.n.* (K); Kund Bangla to Shahid Pani, *Kazmi s.n.* (PES); Siran Valley on the slopes of Musa Ka Musalah, 3000 m., *Kazmi 584* (PES); Mansehra to Garhi Habibullah, *Kazmi s.n.* (PES); Abbottabad, Sherwan hills, *Kazmi 101a* (PES); Batal, *Kazmi s.n.* (PES). KHYBER AGENCY: In jugo Landi Kotal, 700–1000 m., *Rechinger 3034* (W); *Kazmi 2705* (PES). KURRAM AGENCY: Parachinar, 1500–1700 m., *Rechinger 30943* (W); inter Amal Kot et Sadda, 1400 m., *Rechinger 30970* (W). MALAKAND AGENCY: Thana, inter Malakand et Barikot, 700 m., *Rechinger 30465* (W). QUETTA DIST.: In jugo Tak, 30 km. S. Quetta, 2100 m., *Rechinger 28413* (W); inter Bostan et Saran Tangai, 1700–1800 m., *Rechinger 29179* (W); inter Qilla Abdullah et Sheila Bagh, 1600–1900 m., *Rechinger 28978* (W); in jugo Khojak, 2300 m., *Rechinger 29055* (W). Reported from: between Quetta and Ziarat, *Jafri & Akbar 2035* (?).

Kashmir: Below Tragbal, 2100–2400 m., *R. R. Stewart 19428* (GH); Tashgam, Treaty Road, Ladak, 3000 m., *Ludlow & Sherriff 8340* (GH); Matayan to Mechulor, Sept. 1880, *Young s.n.* (BM); Gangangir, Sind Valley, *Ludlow & Sherriff 7959* (BM), 1960 m., *Ludlow & Sherriff 7625* (BM); Bringhi Valley, 1850 m., *Ludlow 12* (BM); Machel, Sapphire mines, Kishtwar, 9270 m., *Ludlow & Sherriff 9124* (BM, GH); Pan Dras, Ladak Road, 3000 m., *R. R. Stewart 10053* (GH-type of var. *kashmiricum*); between Dras and Pindras, west of Dras, 88 road-miles east-northeast of Srinagar, 3000 m., July-Aug. 1928, *Dickason s.n.* (MICH); vicinity of Srinagar, on Sind river, 50 road-miles east-northeast of Srinagar, 3300 m., *Dickason 72* (MICH); Sonamarg, Aug. 6, 1922, *R. R. Stewart s.n.* (K); Sonamarg, Aug. 23, 1922, *R. R. Stewart s.n.* (K); vicinity of Pahlgam, on east of Lidder Valley, 27 road-miles north of Islamabad, 2700 m., *Dickason 74* (MICH); Sind Valley, 5000–7000 ped., Herb. Ind. Or. Hook. f. & Thoms., April 22, 1848, *Thomson s.n.* (K); Bungla, 2700 m., July 24, *C. B. Clarke 29551* (K); (Srinagar), Shalamar Bagh, 1560 m., July 10, 1891, *Gammie s.n.* (K); Nowgung, 2550 m., 18 July, 1876, *C. B. Clarke 29164* (K); Zoji La, 3300 m., *Miss Burtt 220* (E); Zojibal, 3300 m., *Drummond 14202* (E). Miscellaneous: without locality, 1938, *Timmins 1* (BM); Himal. bor. occ., regio temp., 5000–8000 ped., Herb Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH).

Onosma echioides L. (in Hook. Fl. Brit. India **4**: 178. 1883), the name given to the plants belonging to *Onosma hispidum*, by C. B. Clarke is a misidentification.

3. **O. khyberianum** I. M. Johnston, Jour. Arnold Arb. **32**: 211. 1951; Riedl in Rechinger, Fl. Iranica **48**: 178. 1967.

TYPE: WEST PAKISTAN: Khyber Pass, 3700 ft., *H. H. Johnston 22* (E-holotype).

Perennial herb with stout, somewhat knotted roots. Stems solitary to many, usually simple, sometimes branched above, covered densely with unequal, spreading, white trichomes to 6 mm. long, arising from large tuberculate bases, the area between the bases glabrous to puberulous or covered densely with erect, minute trichomes. Basal leaves persistent at anthesis, oblong to oblong-lanceolate, entire, obtuse to subacute, gradually narrowed towards the base, 4–9 cm. long, 5–9 mm. broad, covered on both surfaces with trichomes like those on the stem, midrib inconspicuous above, raised and prominent below; cauline leaves sometimes slightly revolute at the margins, acute, to 4 cm. long, 5–6 mm. broad. Inflorescence of terminal cymes, simple or branched, short and dense in flower, to 5 cm. in diameter, elongated to 18 cm. in fruit, bearing fruiting calyces to 20 mm. apart; bracts lanceolate, roundish at base, broadest in the lower quarter, then gradually narrowed into a long, narrow upper part, acuminate at apex, to 20 mm. long, 2–3 mm. broad in flower, to 30 mm. long, 5–6 mm. broad in fruit. Pedicel 2–4 mm. long in flower, elongated to 13 mm. in fruit. Calyx hairy, divided to the base, lobes lanceolate, attenuate in the upper part, 18–23 mm. long, ± 2 mm. broad in flower, enlarged to 30 mm. long, 3 mm. broad in fruit. Corolla white to cream, externally glabrous to puberulous or bearing some thin, long, trichomes on the lobes, 30–32 mm. long, 2–3 mm. thick at base, gradually widened upwards, 10–12 mm. broad at the top; lobes 2.5–3 mm. broad, recurved. Nectary glabrous, lobed, 0.2–0.4 mm. high. Anthers joined basally and laterally, forming a tube 11–13 mm. long, sterile tips 1.5–2 mm. long, attached to the filaments 3–4 mm. above the anther base; filaments ligulate, dilated towards the base, and decurrent for 5–6 mm., inserted 13–15 mm. above the base of the corolla tube. Nutlets 3–4 mm. long, smooth, shining.

DISTRIBUTION: West Pakistan.

West Pakistan: DIR STATE: Shahi, 2700 m., *Salim 72* (K, PEU). KHYBER AGENCY: Khyber Pass, rocky mountains, 1110 m., *Johnston 22* (E-type); Landi Kotal, 1080 m., *Lowndes L.709* (E); between Ali Masjid and Landi Kotal, ca. 1000 m., *Kazmi 389b* (PES); Landi Kotal to Torkham, near railway bridge, *Kazmi 498a* (PES); Khajuri, *A. J. Ahmad* in *Kazmi s.n.* (PES); Warsak, along the bank of reservoir, *Kazmi 2699* (PES). WAZIRISTAN AGENCY: Between Miram Shah and Razmak, *Kazmi 182b* (PES); without locality, *Duthie 15804* (K).

4. **Onosma griffithii** Vatke, Zeitschr. Gesammt. Naturw. **45**: 127. 1875; Riedl in Rechinger, Fl. Iranica **48**: 178. 1967.

Onosma barbigerum I. M. Johnston, Jour. Arnold Arb. 32: 212. 1951.

TYPE: AFGHANISTAN: without locality, *Griffith 5947* (B-holotype, GH, K, W-isotypes).

Biennial to perennial (?) herb. Stems usually solitary to sometimes few, simple or occasionally with short floriferous branchlets near the top, densely covered with long, stiff, spreading trichomes, to 4 mm. long, arising from tuberculate bases, the area between the bases densely puberulous or covered with thin, minute, spreading trichomes, to 0.2 mm. long. Basal leaves linear, oblong or oblanceolate, entire, roundish to subobtuse, gradually narrowed towards the base, 6–12 cm. long, 4–17 mm. broad, midrib sunken above, raised and prominent below, indument like that on the stems, long trichomes on the upper surface sometimes subappressed; middle cauline leaves lanceolate, ovate-lanceolate to elliptic-oblong, broadest above the base, base usually roundish or rarely attenuated, 3–5 cm. long, to 15 mm. broad; upper cauline leaves reduced in size, subacute. Inflorescence of terminal cymes, simple to sometimes forked, scorpioid, 3–6 mm. in diameter in flower, elongated to 12 cm. in fruit; bracts lanceolate, acute. Pedicels very short, to 2 mm. long in flower, erect, densely hairy, elongated, especially those of the lower fruits, to 6(–10) mm. Calyx divided nearly to the base, lobes linear to linear-lanceolate, 15–20 mm. long, 1–1.5 mm. broad in flower, acute, enlarged to 18–20 mm. long, 2–4 mm. broad in fruit, covered with long spreading trichomes. Corolla yellow, cylindrical-campanulate, glabrous or with few scattered trichomes outside, 22–30 mm. long, 2–3 mm. thick at base, gradually widened upwards, becoming 7–9 mm. in diameter below the sinus, lobes broadly triangular. Nectary narrowly lobulate, glabrous, less than 0.5 mm. high. Anthers united basally and laterally to form a tube, 9–12 mm. long, connectives thickened, muriculate; filaments ligulate, 6–9 mm. long, decurrent base 4–7 mm. long, inserted 10–15 mm. above the base of the corolla tube. Style filiform, shorter than the corolla. Nutlets sparsely verruculose, shining, to 6 mm. long.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: JHELUM DIST.: Salt Range, Sekesar, 22.3.1851, *Fleming 31* (E), *A. J. Ahmad s.n.* (PES). QUETTA DIST.: between Qilla Abdullah and Sheila Bagh, ca. 2400 m., *Kazmi 1537* (PES); Quetta to Chaman, Khojak Pass, above Sheila Bagh, *Lamond 1072* (E); Quetta, 1888, *Duthie 8682* (DD, GH-photograph, E-holotype of *O. barbigerum*); Moorga-Hindubagh, without collector's name, *18925* (DD, GH-photograph); Hanna Valley, 2400 m., 3 May 1888, *Lace 3776* (E); Quetta, *Lace s.n.* (E-mounted with *Lace 3776*); on way from Ziarat to Quetta, 2400 m., *Jafri & Akbar 2035* (BM, E); Tak Pass, on Quetta-Mastung Pass, *Kazmi 1298* (PES); environ de Quetta, *Schmid 1569* (BM); Chiltan, *Kazmi 1566* (PES). WAZIRISTAN AGENCY: Razani, 2700 m., April 1924, *Lester-Garland s.n.* (GH-photograph, K). Reported from: Baluchistan, 1891–1894, *Elliot s.n.* (DD); *Stocks 1137* (DD); Waziristan, *Harsukh 15805* (DD); Chitral, *Harriss 16404* (DD).

I. M. Johnston (l. c.) described *Onosma barbigerum* from Baluchistan, on the basis of Duthie's collection *8682* at the Dehra Dun Herbarium.

He distinguished his species by its broadly elliptic-ovate middle cauline leaves with antrorsely appressed trichomes on the dorsal surface and its shorter corolla, compared to the narrow middle cauline leaves with spreading trichomes on the upper surface and the longer corolla of *Onosma griffithii*. Both the form of middle cauline leaves and the length of the corolla are very variable in the specimens cited above and *O. barbigerum* represents only the form with broadest middle cauline leaves. As there is no correlation between the width of leaves, length of corollas and the appressed or spreading type of trichomes, *O. barbigerum* hardly deserves specific or even varietal recognition.

Onosma griffithii is closely related to *O. khyberianum* and *O. hispidum*. It is distinguished from the former by having much broader bracts not attenuated above, and from the latter in having much shorter basal leaves. The plants belonging to *O. hispidum* have strong perennial roots and stems to 75 mm. long, whereas *O. griffithii* has biennial and short-lived roots with stems never exceeding 35 cm. in length.

5. **O. hypoleucum** I. M. Johnston, Jour. Arnold Arb. 32: 220. 1951.

TYPE: INDIA: without locality, Herb. Late East India Company, *Falconer, s.n.* (GH-holotype).

Erect perennial herb with a stout woody root. Stems usually several, simple or branched in the upper part, to 50 cm. long, 1–2.5 mm. thick and woody at base, densely covered with thin, white, antrorsely appressed trichomes, 0.1–0.4 mm. long, not arising from tuberculate bases, intermixed sparingly to profusely with long, stiff, spreading trichomes, with tuberculate bases, 1–1.3 mm. long. Basal leaves drying and disappearing at anthesis; middle cauline leaves sessile, lanceolate to linear-lanceolate, broadest at base, margins slightly revolute, acute, 1–3 cm. long, 1.5–5 mm. broad, nerve on the upper surface inconspicuous, below raised and prominent; upper surface covered uniformly with short and long, antrorsely appressed trichomes, lower surface densely covered with short, antrorsely appressed trichomes, with only few long trichomes tuberculate at base on the margins and midrib; upper cauline leaves shorter and narrower. Inflorescence usually terminal, sometimes axillary on peduncles, 1–3 cm. long, dense, ca. 2 cm. in diameter in flower, elongated at maturity, sometimes to 12 cm. long; bracts leaflike, smaller, comparatively broader at base. Pedicels slender, densely hairy, to 5 mm. long in flower, to 10 mm. long in fruit. Calyx divided to the base, lobes linear, acute, densely hairy, trichomes like those on the stem, equalling or sometimes slightly surpassing the flowers, to 11 mm. long in flower, not or slightly elongated in fruit, to 13 mm. long. Corolla blue, campanulate, externally densely covered with minute, antrorsely appressed trichomes, inside villous 1.5–2.5 mm. above the base, 10–11 mm. long, 2 mm. thick at the base, gradually widened upwards, 4–5 mm. in diameter just below the sinus, lobes at the margins slightly revolute, 1–2.5 mm. broad, 1–1.5 mm. long. Anthers joined basally and laterally forming a tube exserted from the corolla tube

for more than half its length, 9–10 mm. long, sterile tips 1–1.5 mm. long; filaments gradually widened upwards from the base and then gradually narrowed towards the apex, 6–7 mm. long at base, 0.3–0.5 mm. broad, 0.5–1 mm. above the base, 0.5–0.7 mm. broad, villous for the lower 1–2 mm., inserted 1.5–2 mm. above the corolla base. Nectary lobate, 0.1–0.3 mm. high, villous. Style glabrous, to 15 mm. long. Nutlets shining, minutely rugulose, 2.5–3 mm. long.

DISTRIBUTION: West Pakistan, Kashmir, northwestern India.

West Pakistan: HAZARA DIST.: Thandiani, 2550 m., *R. R. Stewart 27788* (MICH), *Nasir s.n.* (E), *Kazmi 2746* (PES); Kalabagh, ca. 2700 m., *Kazmi 2770* (PES); Nathiagali, near Government House, ca. 2200 m., *Kazmi 2763* (PES); between Nathiagali and Dungagali, ca. 2700 m., *Kazmi 99b* (PES); Changlagali to Dungagali, 2500–2600 m., *R. R. Stewart 23521* (GH), *23521a* (US); Dungagali, *R. R. Stewart 28753* (E); Changlagali, 1950 m., *R. R. Stewart 2956* (K); Aug. 1880, *Young s.n.* (BM); between Mansehra and Garhi Habibulla, *Kazmi 107a* (PES); between Garhi Habibullah and Balakot, *Kazmi 391* (PES); Kaghan Valley, climb from Kewai to Shogran Rest House, *Kazmi 2210a* (PES); hills on east of Kaghan Village, 2000 m., *Kazmi 2217* (PES); Siran Valley, near Jabori, *Kazmi s.n.* (PES). RAWALPINDI DIST.: Murree Hills, Upper Topa, 2500 m., *Kazmi 75b* (PES); on Lower Topa-Patriata Road, near Patriata, *Kazmi s.n.* (PES); Murree-Kohala road, *Kazmi s.n.* (PES).

Kashmir: MUZZAFFARABAD DIST.: Kishanganga Valley, Nilam, *Kazmi s.n.* (PES).

6. **O. thomsonii** C. B. Clarke in Hook. f. Fl. Brit. India **4**: 178. 1883; I. M. Johnston, Jour. Arnold Arb. **32**: 346. 1951.

TYPE: Banahal, southern Kashmir, 6000 ft., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (K-holotype, G-isotype, as *Onosma* No. 3).

Perennial herb. Stems many, erect or ascending, arising from a loosely branched fruticose caudex, 2–3 mm. thick towards the base, simple or branched, 15–50 cm. long, densely covered with slender, white crisped, spreading trichomes, 1–3 mm. long, arising from minute tuberculate bases, usually intermixed with very short, thin, spreading trichomes. Basal leaves drying and disappearing at anthesis; lower cauline leaves numerous, lanceolate to linear-lanceolate, slightly revolute at margins, acute, nerve on the upper surface inconspicuous, raised and prominent below, 5–10 cm. long, 5–10 mm. broad, upper surface grayish-green, covered uniformly with stout, pungent, subpatent, white trichomes, to 1.5 mm. long arising from large tuberculate bases, area between the bases bearing minute, thin, ± subappressed trichomes not exceeding 0.2 mm. in length; lower surface white, totally covered with soft, slender, subpatent trichomes, to 3 mm. long, with long, pungent, stiff trichomes tuberculate at the base only on the midrib and margins; upper cauline leaves usually linear-lanceolate, 2–5 cm. long, 2–9 mm. broad, gradually reduced upwards. Inflorescence of terminal scorpioid cymes, when young 1.5–3 cm. in diameter, at maturity loosely racemose, 9–10 cm. long, frequently forked; bracts leaf-like much smaller, lanceolate, acute, broadest at the base. Pedicels

slender, hairy, 1–3 mm. long in flower, 3–10 mm. long in fruit. Calyx divided to the base, lobes lanceolate, acute, densely villous or villous hispid, 8–10 mm. long in flower, not at all to slightly elongate in fruit. Corolla blue, narrowly-campanulate, 10.5–12 mm. long, 2–2.5 mm. thick at base, widened into an elongate throat, 3–4.5 mm. in diameter, externally densely strigulose, trichomes minute, retrorsely appressed, glabrous inside, throat longitudinally tightly infolded below each corolla sinus, lobes triangular, 1.5 mm. broad, 1 mm. long, tips recurved. Anthers united laterally, forming a tube long exserted from the corolla, 7–8.5 mm. long, sterile tips 1–2 mm. long; filaments subulate, broadest near the base, not decurrent, 6–7 mm. long, arising 3–3.5(–4) mm. above the corolla base. Nectary narrowly lobulate, 0.1 mm. high, villulose. Style 12–17 mm. long, glabrous. Nutlets shining, obscurely rugulose or nearly smooth, 2.5–3.5 mm. long.

DISTRIBUTION: West Pakistan, Kashmir, northwestern India.

West Pakistan: HAZARA DIST.: Thandiani, 2700 m., *Kazmi 392b* (PES); between Thandiani and Kalabagh, 2400 m., *Kazmi 439b* (PES); from Murree north to Nathiagali via Changlagali, 2500–2700 m., *Dickason 71* (MICH); between Barian and Changlagali, *Dickason 70* (MICH); Barian-pipeline, between Murree and Changlagali, *Dickason 75* (MICH); below Kalabagh, 1650 m., *R. R. Stewart 28754* (E); Abbottabad to Nathiagali, above Thai barrier, *Burtt B492* (E); Abbottabad, hill above Kehal near the top, 1500 m., *Kazmi 550* (PES); Abbottabad to Sherwan, ca. 1500 m., *Kazmi s.n.* (PES); between Dadar and Jabori, *Kazmi 589b* (PES); Kaghan Valley, Balakot, *Jafri s.n.* (E); between Balakot and Kewai, *Duthie 19479a* (GH); Mahandri to Kaghan Village, *Kazmi 642a* (PES); Shogran to Paya, 3000 m., *Kazmi 2486* (PES); Siran Valley, between Jabori and Shahid Pani Rest House, *Kazmi s.n.* (PES). MALAKAND AGENCY: between Dargai Post and Malakand village, *Kazmi s.n.* (PES). RAWALPINDI DIST.: Upper Topa to Kashmiri Bazar, *Kazmi 2846* (PES); Jhikagali to Lower Topa, *Kazmi 108b* (PES); Ghoragali to Murree, *Kazmi 2829* (PES); Barian, Murree Hills, *R. R. Stewart 7123* (K); Murree, 20 May 1938, *Madan Gopal s.n.* (MICH). SWAT STATE: Saidu Sherif towards Maina, 1000 m., *R. R. Stewart 27443* (K). Miscellaneous: Punjab, Bassahi, *Drummond 26013* (E).

Kashmir: MUZZAFFARABAD DIST.: Dhanni to Titwal, 1000 m., *R. R. Stewart 17371* (GH); Dhanni, 1130 m., *Schmid 1655* (BM, MICH, RAW); between Garhi Habibullah and Muzzaffarabad, *Kazmi 290b* (PES).

7. **O. bracteatum** Wall. in Roxb. Fl. Indica, ed. Carey **2**: 13. 1824; DC. Prodr. **10**: 66. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 178. 1883.

Onosma bracteatum Wall. Cat. No. 936. 1829, *nomen nudum*.
Onosma macrocephala D. Don, Prodr. Fl. Nepal. 99. 1825. Gen. Syst. **4**: 316. 1838.

TYPE: "Shree-nugur" (Srinigar), *Kamroop*, Wall. Cat. No. 936 (K).

Perennial herb. Stems brownish, usually many, arising from a persistent cluster of basal leaves, simple, leafy, to 50 cm. long, 4–6 mm. thick at the base, covered with intermixed short, thin, crisped trichomes not tubercu-

late at the bases and long, moderately stiff spreading trichomes with large tuberculate bases; short trichomes 0.2–0.6 mm. long, long ones 1.4–4 mm. long. Basal leaves persistent at anthesis, lanceolate, entire, acute, gradually narrowed towards the base into a winged petiole, 3–5 mm. wide, including petioles 6–8 mm. long, 15–35 mm. broad, veins evident, green above, greenish-white below, both surfaces covered with short and long types of trichomes, to 1.5 mm. long; middle cauline leaves lanceolate, broadly sessile, entire, acute, rounded at the base, 6–8 cm. long, 1–2.7 cm. broad; upper cauline leaves reduced upwards. Inflorescence of terminal glomerate clusters, very dense, 4–10 cm. broad in flower, later becoming lax, revealing the crowded densely flowered, forked individual cymes; bracts hairy, lanceolate, with acuminate, very prolonged, slender tips. Pedicels 3–5 mm. long in flower, 8–12 mm. long in fruit. Calyx divided nearly to the base, lobes linear-lanceolate, acuminate, 15–18 mm. long in flower, covered densely with spreading trichomes to 1–5 mm. long, elongated to 25 mm. in fruit. Corolla blue (*fide* Duthie), bearing loose, long, crisped, slender trichomes externally above the middle, glabrous inside except on the nectary, usually shorter to sometimes equalling the calyx, 13–17.5 mm. long, 3 mm. thick at the base, gradually a little widened upwards, 4–5 mm. broad below the sinus; lobes triangular, 2–3 mm. broad, 1–1.5 mm. high, weakly revolute at the margins. Anthers joined only at base, 6–7 mm. long, sterile tips weakly developed, 0.5–0.8 mm. long; filaments 2–2.5 mm. long, attached 5.5–6.5 mm. above the corolla base, decurrent base swollen, fusiform, 3.5–4 mm. long, marked by fusiform depressions on the outside of the corolla. Nectary a weakly lobed collar, densely villous on inner side. Style glabrous, 9–13 mm. long. Nutlets gray, angulate, coarsely rugose and tuberculate, 4–4.5 mm. long.

DISTRIBUTION: Kashmir, northwestern India.

Kashmir: Srinagar, *Kamroop* in *Wallich 936* (K).

Onosma bracteatum is very distinct from the other species of *Onosma* in our area in having anthers coherent only at the base, corolla usually much shorter than the calyx, and upper cauline leaves and bracts broadly lanceolate and narrowed into long attenuated tips.

8. **O. dichroanthum** Boiss. Diagn. Pl. Orient. Nov. I. 2(11): 107. 1849; Riedl in Rechinger, Fl. Iranica **48**: 180. 1967.

Onosma setosum β dichroanthum (Boiss.) Boiss. Fl. Orient. **4**: 181. 1875.

TYPE: Iberia prope Baku, *C. A. Meyer s.n.* (G).

Biennial or very short lived perennial herb. Stems usually several, erect or ascending, simple or branched above to 75 cm. long, 3–15 mm. thick at base, branches to 20 cm. long, covered densely with very short, thin trichomes, 0.1–0.2 mm. long, and stiff spreading, unequal trichomes tuberculate at base, to 5 mm. long. Basal leaves usually dried at anthesis, clustered, linear to linear-oblanceolate, entire, obtuse, 10–20 cm. long,

4–15 mm. broad, covered on both surfaces with trichomes like those on the stems, usually shorter, sometimes hairy only on the midrib and the margins below; middle cauline leaves oblong-lanceolate, obtuse to subacute to 10 cm. long, 15 mm. broad; upper cauline leaves gradually reduced upwards. Inflorescence of terminal racemes, short, scorpioid in flower, 5–6 cm. in diameter, lax, elongate in fruit, 10–15 cm. long; bracts lanceolate, especially the lowermost. Pedicels densely hairy, ca. 5 mm. long in flower, 10–15 mm. long in fruit. Calyx divided nearly to the base, lobes linear to linear-lanceolate, acute, covered densely with long, ± antrorsely subappressed trichomes, 15–25 mm. long in flower, elongated to 25–30 mm. in fruit. Corolla yellow, cylindrical-campanulate, externally glabrous except for tuft of hairs near the tip of the lobes, 25–40 mm. long, 2.5–3 mm. thick at base, gradually expanding and becoming 10 mm. thick just below the sinus; lobes deltoid, 2.5–4.5 mm. broad, recurving. Anthers joined at the base, 9–12 mm. long, sterile tips 1–1.5 mm. long, connectives swollen, muriculate; filaments linear, 3.5–4.5 mm. long, arising 17–20 mm. above the corolla base, base decurrent for about 10 mm. Nectary a slightly lobed, glabrous collar, 0.3–0.8 mm. high. Style 25–33 mm. long. Nutlets pale, shining, smooth or slightly roughened, 4–5 mm. long.

DISTRIBUTION: Turkestan, Afghanistan, West Pakistan.

West Pakistan: HAZARA DIST.: 5 miles from Dadar, on Abbottabad-Dadar road, *Kazmi 60b* (PES); Mansehra, *Nasir 1659* (K), *Kazmi 568b* (PES); between Gahri Habibullah and Balakot, *Kazmi 2749* (PES); between Abbottabad and Thandiani, *Kazmi 853* (PES). KOHAT DIST.: on top of the pass, between Peshawar and Kohat, 15 miles from Kohat, *Kazmi 2651* (PES). KURRAM AGENCY: Amal kot to Sadda, ca. 15 km. from Parachinar, 1400 m., *Lamond 1900* (E); without locality, *Afandi 244* (PES); Parachinar, *Kazmi 2612* (PES), *A. Rehman in R. R. Stewart 25906* (BM); Shalozan, *Kazmi s.n.* (PES). MALAKAND AGENCY: between Dargai Check Post and Malakand village, *Kazmi 2586* (PES). QUETTA DIST.: Gwal, 1800 m., 27 April 1888, *Lace s.n.* (E); Zandara (Ziarat), 2400 m., *Jafri & Akbar 2196* (E); Ziarat, 2100 m., *Santapau 6449* (GH); Kach-Ziarat road, 2100 m., *R. R. Stewart 550* (MICH); 10 miles before Ziarat, on Quetta-Ziarat road, *Kazmi 1658* (PES). SWAT STATE: Mingora, 900 m., *S. Ali 26149a* (BM). WAZIRISTAN AGENCY: 2 miles to Miram Shah, on Bannu-Miram Shah road, *Kazmi 211b* (PES); between Miram Shah and Razmak, ca. 1350 m., open stony hillside and Nullah bank, *Lowndes 644* (E). Reported from: Baluchistan, Kawas Pangi, 1800 m., April 30, 1893, *Munro s.n.* (DD). CHITRAL STATE: Chitral, 1896, *Hamilton s.n.* (DD), 1894, *Younghusband s.n.* (DD); Chitral, 1450 m., June 2, 1895, *Harriss s.n.* (DD); Guirat (Ziarat?) to Chitral, 1450 m., May 31, 1895, *Harriss s.n.* (DD); Broz, 2540 m., June 6, 1895, *Harriss s.n.* (DD); Drosh, Chitral, 1350 m., 1908, *Toppin 110* (K); Gilgit, Kaghusi, Gilgit Expedition 1650 m., June 30, 1881, *Giles 375* (DD); Hazara, Shinkiyari, June 3, 1899, *Inayat s.n.* (DD); Kurram Agency, Shinnak, Kurram Valley, April 1879, *Aitchison 28* (G); Parachinar, April 14, 1894, *Harriah s.n.* (DD), June 30, 1897, *Harriah s.n.* (DD).

9. **O. limitaneum** I. M. Johnston, Jour. Arnold Arb. **32**: 354. 1951; Riedl in Rechinger, Fl. Iranica **48**: 185. 1967. *pro parte* excl. var. *majus* I. M. Johnston.

Onosma limitaneum var. *parviflorum* I. M. Johnston, Jour. Arnold Arb. 32: 354. 1951.

Onosma johnstonii H. Riedl in Rechinger, Fl. Iranica 48: 183. 1967. *syn. nov.*

TYPE: BALUCHISTAN: Fort Sandeman, without citation of collector's name *18927* (DD-holotype).

Perennial herb. Stems erect to ascending, usually 2–4, sometimes solitary, branched near the base or above, 10–30 cm. long, to 5 mm. thick at base, covered densely with thin, stiff, spreading trichomes, to 0.2 mm. long, intermixed sparsely or profusely with long, thick, pungent, unequal, spreading trichomes, to 5 mm. long, arising from prominent tuberculate bases. Basal leaves numerous, spathulate, linear-spathulate to spathulate-oblanceolate, margins sometimes slightly revolute, obtuse to subacute, gradually narrowed towards the base into a petiole slightly shorter than the lamina, winged and dilated towards the base, 2.5–7 mm. long, 3–7 mm. broad, midrib inconspicuous above, raised and prominent below, upper surface covered ± uniformly, lower surface usually with trichomes on the midrib and margins like those on the stem; cauline leaves sessile, linear-oblong, oblong-lanceolate, or oblong-spathulate, acute to obtuse, usually ± dilated at the base, 14–45 mm. long, 2–7 mm. broad. Inflorescence usually terminal or sometimes lateral, simple or bifurcate, when young strongly scorpioid, dense, 3–4 cm. in diameter, lax at maturity and elongated to 10 cm.; bracts sessile, lanceolate, acute, dilated towards the base, to 12 mm. long, 5 mm. broad above the base. Pedicels slender, hairy, 2–3 mm. long in flower, elongated to 6 mm. in fruit. Calyx divided to the base, lobes linear, acute, 7–8 mm. long in flower, elongated to 11 mm. in fruit, never broader than 1 mm., both surfaces covered, more densely inside and on the margins, with white, stiff, unequal trichomes spreading at the margins and outer surface, appressed inside. Corolla yellow turning purple-yellow-red in time, tubular, externally puberulous, glabrous within, 7–9 mm. long, 1.5–2 mm. thick at base, slightly dilated in the middle, slightly constricted below the sinus, 2–3 mm. in diameter, lobes triangular, longer than broad, ca. 1–1.2 mm. long, suberect to slightly recurved. Anthers linear, joined only at their bases, ca. 3.5 mm. long, sterile tips 0.5 mm. long, biapiculate, included; filaments gradually narrowed upwards, 2–2.5 mm. long, inserted more or less below the middle of the corolla tube. Nectary membranous, lobed, 0.5 mm. high, ciliate. Style glabrous, filiform, not at all to slightly exserted from the corolla, stigma distinct, globular. Nutlets usually one developing, brownish, shining, 3 mm. long, ca. 1.5 mm. broad, areola minute, transversely elliptic.

DISTRIBUTION: Iran, Afghanistan, West Pakistan.

The species is very variable; the following two varieties may be distinguished.

9a. Var. **limitaneum.**

Corolla 7–9 mm. long, externally puberulous, at base 1.5–2 mm. thick, 2–3 mm. in diameter below the sinus, lobes 0.8–1.2 mm. long; anthers 2.5–3.5 mm. long, filaments 1.5–2 mm. long, inserted 3 mm. above the corolla base.

DISTRIBUTION OF VARIETY: Iran, Afghanistan, West Pakistan.

West Pakistan: MAKRAN DIST.: 25 miles from Hushab on Hushab-Panjgur Road, *Kazmi 1184* (PES). QUETTA DIST.: Quetta to Sibi, 1500 m., Bolan Pass, *Lamond 718* (E), *Kazmi 1399b* (PES), *Rechinger 28421* (W); Murdar and Gwal reserve, 1800 m., April 10–12, 1889, *Lace 3794* (DD, E). ZHOB DIST.: Fort Sandeman to Shinghar, 1450 m., barren rocky ground, *Kazmi 1931* (PES), *Lamond 1459* (E), 2050–2300 m., *Rechinger 29878* (W); 30 km. north Fort Sandeman versus Wana, *Rechinger 29857* (W). Reported from: BALUCHISTAN: Kaka in Lora Valley, *Lace s.n.* (?); Gival, 750–900 m., May 6, 1893, *Munro s.n.* (DD); Mina Bazar, 1440 m., May 11, 1896, without collector's name *18928* (DD); Gastoi, May 28, 1897, without collector's name *20600A* (DD); Kharwand, June 7, 1897, without collector's name *20600B* (DD); Sin Kachh, May 12, 1897, without collector's name *20600* (DD).

9b. Var. **majus** I. M. Johnston, Jour. Arnold Arb. **32**: 354. 1951; Riedl in Rechinger, Fl. Iranica **48**: 186. 1967.

TYPE: AFGHANISTAN: Herb. Late East India Company, without locality, *Griffith 5946* (GH-holotype).

Corolla 15–17 mm. long, externally sparsely hispidulous only on the veins, otherwise glabrous, 2–2.5 mm. thick at base, 5–6 mm. in diameter below the sinus, lobes 1.5 mm. long; anthers 5.5–6.5 mm. long, filaments 3.5–4 mm. long, inserted 6–8 mm. above the corolla base.

DISTRIBUTION OF VARIETY: Afghanistan, West Pakistan.

West Pakistan: QUETTA DIST.: Quetta to Chaman, between Qilla Abdullah and Sheila Bagh, 1600–1900 m., *Lamond 1046* (E), *Kazmi 1542a* (PES); between Quetta and Bazuzai, ca. 1500 m., *Kazmi 1538* (PES); Chiltan mountains, near Quetta, *Kazmi s.n.* (PES). Miscellaneous: Baluchistan, *Stocks 997* (DD, GH).

30. **Trichodesma** R. Br. Prodr. Fl. Nov. Holl. 496. 1810, nom. cons.

Pollichia Medic. Bot. Beobacht. 247. 1783.
Borraginoides Moench, Meth. 515. 1794.
Leiocarya Hochst. Flora **27**: 30. 1844.
Streblanthera Steud. Flora **27**: 29. 1844.
Spiroconus Stev. Bull. Soc. Nat. Moscou **24**(1): 576. 1851.
Boraginella Siegesb. ex O. Kuntze. Rev. Gen. Pl. **2**: 437. 1891.

TYPE SPECIES: *T. zeylanicum* (N. L. Burm.) R. Br. *typ. cons.*

Perennial, rarely annual, herb with woody base. Lower leaves usually opposite, upper leaves alternate. Pedicels axillary, 1-flowered, going off into terminal racemes by the gradual reduction of the leaves. Calyx 5-fid to 5-partite, lobes imbricate, ovate to lanceolate, attenuate to cuspidate at

apex, often dilated, cordate or sagittate at the base, enlarged in fruit. Corolla subrotate, hypocrateriform to infundibuliform, faucal appendages lacking, lobes ovate, cuspidate at apex. Stamens 5, anthers large, oblong to linear-lanceolate, convergent into a cone, apices aristate, awns contorted, filaments short, inserted on the corolla tube. Ovary 4-locular, conic-ovoid, not divided in flower. Style filiform, stigma small. Nutlets ovoid, triangular or subglobose, smooth, rugose to hirsute, marginate to emarginate.

Species 40 to 45, distributed in tropical and subtropical Africa, Asia, and Australia.

KEY TO THE SPECIES

a. Nutlets emarginate to indistinctly marginate.
  b. Nutlets glabrous, smooth or rarely slightly rugulose, 4–5 mm. long; calyx sagittate at base in flower, auriculate in fruit, lobes gradually narrowed upwards. ..... 1. *T. indicum.*
  b. Nutlets usually minutely tuberculate, strongly and irregularly rugose, 5–6 mm. long; calyx divided for 2/3 of its length, roundish at base in flower, dilated in fruit, narrowed abruptly upwards. .... 2. *T. incanum.*
a. Nutlets distinctly and broadly marginate.
  c. Wings of the nutlets plane, leaves covered only with long trichomes arising from tuberculate bases, area between the bases glabrous. ..... 3. *T. africanum.*
  c. Wings of the nutlets incurved to inflexed; leaves covered with long trichomes, arising from tuberculate bases, area between the bases puberulous to covered with short, thin trichomes.
    d. Lower cauline leaves short-petiolate, upper cauline leaves sessile, elliptic-oblong, obtuse. ..... 4. *T. stocksii.*
    d. Lower cauline leaves long-petiolate, upper cauline leaves short-petiolate to subsessile, lanceolate to ovate-lanceolate, acute. ..... 5. *T. longipedicellatum.*

1. **T. indicum** (L.) R. Br. Prodr. Fl. Nov. Holl. 149. 1810; A. DC. in DC. Prodr. 10: 172. 1846; Boiss. Fl. Orient. 4: 280. 1875; C. B. Clarke in Hook. f. Fl. Brit. India 4: 153. 1883; Brand, Pflanzenr. IV. 252(Heft 78): 38. 1921; Riedl in Rechinger, Fl. Iranica 48: 226. 1967.

Borago indica L. Sp. Pl. 137. 1753.
Pollichia indica Medicus, Bot. Beobacht. 247. 1783.
Borraginoides sagittata Moench, Meth. 516. 1794.
Borago spinulosa Roxb. Hort. Bengal. 13. 1814.
Trichodesma perfoliatum Wall. Cat. No. 932. 1828, *nomen nudum.*
Trichodesma hirsutum Edgew. Jour. Asiat. Soc. Bengal 21: 175. 1853.

TYPE: Habitat in India Orientale, Herb. No. 188.2 (LINN).

ICON.: Wight, Illustr. Indian Bot. 2: *t. 172, fig. 1–15.* 1850.

Erect annual herb. Stems profusely branched, branches spreading, to 50 cm. long; densely covered with thin, crisped, white trichomes to 0.2

mm. long, intermixed sparsely to profusely with long, stiff, slender, trichomes to 0.5 mm. long, arising from tuberculate bases. Basal leaves drying at anthesis; cauline leaves usually opposite, oblong, lanceolate or rarely ovate, entire, acute to subacute, narrowed, dilated, or amplexicaul at base, to 7 cm. long and 25 mm. broad, covered on both surfaces in various densities with slender, spreading trichomes to 2 mm. long, arising on the upper surface from prominent tuberculate bases, on the lower surface from inconspicuous ones; middle cauline leaves usually larger than the lower and upper cauline leaves. Inflorescence terminal, lax, few flowered; bracts leaflike. Pedicels slender, pubescent, to 25 mm. long in flower, not at all to very slightly elongated in fruit. Calyx divided nearly to the base, lobes oblong, gradually narrowed from the base towards acute apex, at base sagittate-auriculate, to 12 mm. long and 15 mm. broad at base in flower, slightly enlarged in fruit. Corolla pinkish-blue, infundibuliform, slightly surpassing the calyx, 12–14 mm. long, lobes semiorbicular, spreading, abruptly narrowed to filiform apices. Anthers densely villose, aristate, awns equalling the anthers, glabrous, strongly contorted. Nutlets ovoid, glabrous, smooth or rarely slightly rugulose, white to bluish, 4–5 mm. long.

DISTRIBUTION OF SPECIES: Afghanistan, West Pakistan, Kashmir, India, Philippines, and Mauritius.

A very variable species in its habit, leaf shape, and density of trichomes on the stem and leaves. The following two varieties may be distinguished.

1a. Var. **indicum**.

Stem and leaves densely covered with trichomes; cauline leaves broad, more or less dilated at base, not amplexicaul.

DISTRIBUTION OF VARIETY: As that of species.

West Pakistan: ATTOCK DIST.: Campbellpore, 350 m., *Kazmi 2737* (PES). DERA ISMAIL KHAN DIST.: Dera Ismail Khan to Tank, *Kazmi 357b* (PES). JHELUM DIST.: between Rawalpindi and Jhelum, 10 miles from Jhelum, *Kazmi 2526a* (PES). HAZARA DIST.: Abbottabad, hill above Kunj, 1200 m., *Kazmi 102b* (PES); between Havelian and Abbottabad, 5 miles from Havelian, *Kazmi 51a* (PES); Sherwan Road, Abbottabad, 1200 m., *Kazmi 201a* (PES); Mansehra, 1000 m., *Kazmi 569a* (PES); Batrasi, 1060 m., *Kazmi 577b* (PES); 6 miles from Garhi Habibullah towards Muzzaffarabad, 1100 m., *Kazmi 819a* (PES); Balakot, *Jafri & Ali 3283* (E); between Balakot and Kiwai, *Kazmi s.n.* (PES); 5 miles from Haripur, between Haripur and Mirpur, *Kazmi 680b* (PES). KOHAT DIST.: 5 miles from Kohat on Kohat-Bannu road, *Kazmi 2472* (PES); 14 miles from Kohat on Kohat-Peshawar road, *Kazmi 2492* (PES); between Kohat and Khushalgarh, 1000 m., *Kazmi 2588* (PES). MARDAN DIST.: Dargai, near Hydro-Electric Works, *Kazmi s.n.* (PES). MALAKAND AGENCY: Road to Swat, 800 m., *Lamond 1648* (E), *Rechinger 30448* (W). MIANWALI DIST.: Kalabagh, *Kazmi 2578* (PES). PESHAWAR DIST.: between Jamrud and Warsak, 350 m., *Kazmi 2710* (PES); near Michni bridge, 400 m., *Kazmi s.n.* (PES). RAWALPINDI DIST.: Islamabad, Paracharian Hill, *Kazmi 2835* (PES); Rawalpindi to Kahuta by Saon Road, *Burtt*

1110 (E); Topi Park, *Kazmi s.n.* (PES); Dhamyal near Rawalpindi, 500 m., 30 March, 1940, *R. R. Stewart s.n.* (GH); near Chaklala Railway Station, *S. H. Abid in Kazmi s.n.* (PES); environs of Rawalpindi, *Schlagintweit 10892* (E). SWAT STATE: Swat Valley, 1100 m., *Weatherhead 3, 96* (BM); Kalangai, *Weatherhead 15* (BM); inter Mingora et Khwazakhiela, 850–950 m., *Rechinger 30519* (W); Buttkhela, 900 m., *M. A. Siddiqui 27112* (BM, RAW). Miscellaneous: Mera to Marri, 1500–1800 m., *Schlagintweit 11509* (GH); Punjab, without locality, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH). Reported from: Las Bela, *Hughes-Buller, 18777*; Baluchistan, Bsit. *Blater & Hallberg s.n.* (?).

Kashmir: Domel, Jhelum Valley, 800–900 m., *Ludlow & Sherriff 8060* (GH); between Baramulla and Kohala, Oct. 19, 1913, *Evershed s.n.* (BM); Mirpur, *Kazmi 517* (PES); Muzzaffarabad, *Kazmi 305a* (PES). Miscellaneous: Western Himalaya, without locality, *Duthie s.n.* (A).

1b. Var. **amplexicaule** (Roth) Cooke, Fl. Bombay Presidency **2**: 215. 1904.

Trichodesma amplexicaule Roth, Nov. Pl. Sp. 104. 1821; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 153. 1883.
T. indicum var. *amplexicaule* (Roth) Sedgwick, Rec. Bot. Surv. India **6**(8): 350. *t. XI.* 1919.

TYPE: Not seen.

Stem sparsely covered with trichomes; leaves with the upper surface uniformly covered with trichomes with large tuberculate bases; the lower surface with similar trichomes confined to midrib and veins; cauline leaves broad at the base, ± subcordate, subamplexicaul.

DISTRIBUTION OF VARIETY: South India, Ceylon, West Pakistan.

West Pakistan: KARACHI DIST.: Malir Cantonment, *Burtt 131560* (E); Mango Pir, *A. Rehman 25713* (BM); Malir, *Jafri 2534* (E).

2. **T. incanum** (Bunge) A. DC. in DC. Prodr. **10**: 174. 1846; Bunge, Mém. Acad. Pétersb. Sav. Étr. **7**: 417. 1854; Boiss. Fl. Orient. **4**: 282. 1875; Brand, Pflanzenr. IV. **252**(Heft 78): 36. 1921, excl. var. *griffithii* & f. *aitchisoni*; M. Pop. Fl. URSS **19**: 691. 1953; Riedl in Rechinger, Fl. Iranica **48**: 223. 1967.

Friedrichsthalia incana Bunge, Del. Sem. Hort. Dorpat. 7. 1843.
Trichodesma molle A. DC. in DC. Prodr. **10**: 174. 1846.
Spiroconus glaucus Stev. Bull. Soc. Nat. Moscou **24**(1): 577. 1851.
Trichodesma strictum Aitch. & Hemsl. Jour. Linn. Soc. Bot. **19**: 178. 1882.
Boraginella incana O. Kuntze, Rev. Gen. Pl. **2**: 436. 1891.
Boraginella stricta (Aitch. & Hemsl.) O. Kuntze, *ibid.*
Boraginella mollis (DC.) O. Kuntze, *ibid.*
Trichodesma molle DC. var. *strictum* (Aitch. & Hemsl.) Brand, Pflanzenr. IV. **252** (Heft 78): 37. 1921.

TYPE: In collibus prope Samarkand, *Lehmann s.n.* (LE, P).

Perennial herb or undershrub. Stems erect, ascendent to sometimes pro-

cumbent, profusely branched, branches to 100 cm. long, covered densely with thin, slender, crisped, retrorsely subappressed, white trichomes 0.2–0.5 mm. long, intermixed sparsely with thick, pungent, spreading trichomes to 1 mm. long, arising from tuberculate bases. Basal leaves drying at anthesis, lower cauline leaves sessile, ovate, elliptic to oblong, entire, acute, dilate-rotundate to sometimes subcordate at base, 2.5–10 cm. long, (10–)15–35(–60) mm. broad, sparsely covered above with white, slender, spreading to subappressed trichomes, 3–5 mm. long, more frequently intermixed with longer trichomes with tuberculate bases, lower surface densely covered with short spreading trichomes, less frequently intermixed with longer ones; upper cauline leaves shorter and narrower. Inflorescence terminal, simple or bifurcate, lax, few-flowered; bracts minute, linear. Pedicels slender, hairy, 2.5–3 cm. long in flower, not elongated in fruit. Calyx divided 2/3 its length, lobes ovate, long-attenuate towards the acute apex, roundish at base, densely pubescent, 14–20 mm. long in flower, slightly enlarged and dilated at base in fruit. Corolla blue, tube 7–8 mm. long, limb patent, 20–25 mm. in diameter, lobes ovate, abruptly narrowed to the linear apex. Anthers villous, aristate, awns glabrous, ± equalling the anthers. Nutlets emarginate to inconspicuously marginate, irregularly strongly rugose and minutely tuberculate on the dorsal surface, 5–6 mm. long.

DISTRIBUTION: Iraq, Iran, Afghanistan, West Pakistan, Turkestan.

West Pakistan: KURRAM AGENCY: Kurram Valley, Ali Khel, 2250 m., 1879. *Aitchison 864* (GH).

Very common in Afghanistan and Turkestan, *Trichodesma incanum* is known from West Pakistan only from the collection cited above. It is distinguished from the other species of our area by its densely pubescent, sessile, ovate, acuminate leaves and its rough, rugose, and tuberculate nutlets.

3. **T. africanum** (L.) R. Br. Prodr. Fl. Nov. Holl. 496. 1810; Lehm. Asperif. 195. 1818; DC. Prodr. **10**: 173. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 154. 1883; Boiss. Fl. Orient. **4**: 1875; Brand. Pflanzenr. IV. 252(Heft 78): 29. 1921; Riedl in Rechinger. Fl. Iranica **48**: 220. 1967.

Borago africana L. Sp. Pl. 138. 1753.
Borrago verrucosa Forssk. Fl. Aegypt.-Arab. 41. 1775.
Pollichia africana Medic. Bot. Beobacht. 247. 1783.
Borraginoides aculeata Moench, Meth. 260. 1794.
Boraginella africana O. Kuntze, Rev. Gen. Pl. 2: 435. 1891.
Boraginoides africana Hiern. Cat. Afr. Pl. Welw. 3: 721. 1898.
Trichodesma africanum var. *homotrichum* Brand. Pflanzenr. IV. **252** (Heft 78): 30. 1921.

TYPE: Habitat in Aethiopia, Herb. No. 188.4 (LINN).

Annual or biennial herb with woody base. Stems fistulous, usually many, erect to ascending, usually branched, branches to 100 cm. long and 1 cm. thick at the base, densely covered with prickly, stiff, thick trichomes, 0.5–2 mm. long, with large calcareous tuberculate bases, area between the bases glabrous, trichomes falling with age. Basal leaves petiolate, lamina ovate, lanceolate-ovate to rarely oblong, acutish, including petioles 2.5–9 cm. long, 12–30 mm. broad, midrib sunken above, prominent below, densely covered on the upper surface, sparsely so on the lower surface (except the nerves) with trichomes more or less like those on the stem; cauline leaves short petiolate, subopposite; upper cauline leaves sessile, gradually reduced in size upwards. Inflorescence terminal or axillary, lax. Pedicels slender, densely covered with trichomes, very short to 5 mm. in flower, elongated to 15 mm. in fruit. Calyx divided nearly to the base, lobes broadly lanceolate, broadest at the truncate or subcordate base, gradually attenuate towards the prolonged acute apex, 5–6 mm. long and 2.5–3 mm. broad, with a prominent midrib, enlarged to 10 mm. long, 5–6 mm. broad, with conspicuous cordate-auriculate base and shorter tips in fruit; externally densely covered on the midrib and the margins with stiff, spreading trichomes, and with soft, thin, antrorsely appressed trichomes within. Corolla bluish-white to light blue, small, tube shorter than the calyx, lobes triangular ovate, ± twice as long as the tube, attenuate, acute, subpatent at apex. Anthers villous, awns glabrous. Style shorter than the calyx. Nutlets brownish, triangular ovate, carinate, dorsally tuberculate, margined, margins plane, denticulate, 2–4 mm. long.

DISTRIBUTION: Africa, Arabia, Iran, Afghanistan, West Pakistan, India.

West Pakistan: DADU DIST.: Karachi to Dadu, Thano Bula Khan to Kotri, *Lamond 1818* (E), *Rechinger 28653* (W), *Kazmi 1406b* (PES), open slopes. *Lamond 817* (E). KALAT DIST.: Sibi to Quetta, below Mach, rocky roadside slopes, *Lamond 876* (E); infra Mach versus Ab-i-Gum, *Rechinger 28482* (W). MAKRAN DIST.: 20 km. W. Hushab, *Rechinger 28026* (W), *Kazmi 946b* (PES). Miscellaneous: Sind, *Stocks 375* (GH). Reported from: Sind, *Stocks 575*; Thano Bula Khan, *Woodrow*; Laki, *Woodrow* (Cooke, Fl. Bombay Pres. 2: 216. 1904).

4. **T. stocksii** Boiss. Diagn. Pl. Orient. Nov. II. 3(3): 140. 1856; Fl. Orient. 4: 282. 1875. Burkill, Fl. Pl. Baluchistan 51.1909; Riedl in Rechinger, Fl. Iranica 48: 222. 1967.

TYPE: Pakistan: "In regione *Beloutschistan*," *Stocks s.n.* (G-holotype, K).

Perennial herb. Stems decumbent, branched, branches axillary, 30 cm. or more long; stem and branches densely covered with thin, short trichomes, intermixed with thick, stiff trichomes arising from tuberculate bases. Leaves oblong-elliptic, obtuse, attenuate towards the base; lower cauline leaves short petiolate, covered with trichomes similar to those on the stem. Inflorescence subcorymbose, 3–5-flowered; bracts minute, linear-lanceolate. Pedicels long in fruit. Calyx 10–12 mm. long, lobes cordate-

rotundate at the base, enlarged in fruit. Corolla campanulate, hardly longer than the calyx, lobes short ovate, abruptly acuminate and recurved at apex. Anthers densely lanate, aristate, awns slightly contorted. Nutlets pitcherform, subglobose, margins membranaceous, strongly inflexed.

DISTRIBUTION: South Iran, West Pakistan.

West Pakistan: Gandava, lower Baluchistan, *Stocks s.n.* (G, K).

I could not examine the type or any other specimen of *Trichodesma stocksii* from Pakistan or Iran. The description given above is according to Boissier (*l. c.*).

5. **T. longipedicellatum** Rech. f. & H. Riedl in Rechinger, Fl. Iranica **48**: 222. 1967.

TYPE: Pakistan: Inter Awaran et Turbat, in alveo lapidoso, 100–200 m., 11. IV. 1965, *K. H. Rechinger 27760* (w-holotype).

ICON.: Riedl, l. c. *t. 38, 39.* 1967.

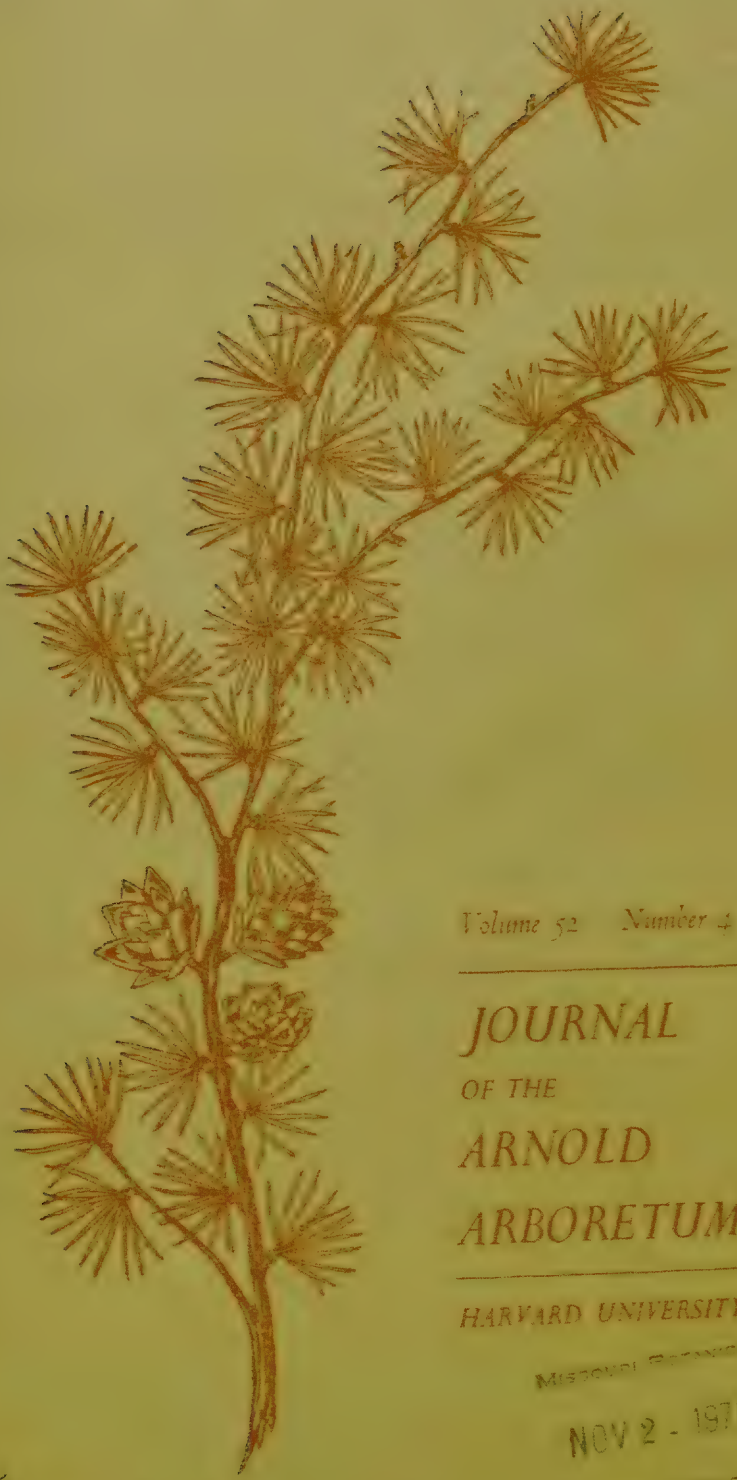
Annual (?) or perennial herb. Stems flaccid, angulate, herbaceous, branched, branches axillary, spreading, to 60 cm. long, covered with thin, crisped, retrorsely subappressed, white trichomes, to 0.2 mm. long, not tuberculate at base, sparsely intermixed with thick, prickly, spreading trichomes to 0.5 mm. long, arising from tuberculate bases, falling with age. Leaves petiolate, lanceolate to ovate-lanceolate, entire, obtuse to subacute, attenuate at base, including the petioles 2–9 cm. long, 7–40 mm. broad, densely covered on both surfaces with thin, short trichomes, intermixed profusely on the upper surface and sparsely on the lower surface with thick trichomes similar to those on the stem; upper cauline leaves short-petiolate to sessile, narrower and shorter, usually acute. Inflorescence terminal or axillary, lax, few-flowered; bracts minute. Pedicels flexuous, densely hairy, 12–15 mm. long in flower, elongated to 20 mm. in fruit. Calyx divided to the base, lobes broadly lanceolate, gradually attenuate towards the prolonged acute apex, roundish at base, 8.5–9.5 mm. long and 3.5–4.5 mm. broad above the base in flower, densely covered with short trichomes, intermixed usually at the midrib and margins with thick trichomes tuberculate at the base, triangular ovate, to 12 mm. long, 9 mm. broad, slightly connate at base in fruit. Corolla mauve, white and almost tan in the center, ca. 18 mm. in diameter in dried specimens, tube shorter than the calyx, lobes spreading obtuse, ca. 7 mm. long. Anthers densely white-villous, aristate, awns contorted, glabrous. Style filiform, after anthesis 10–15 mm. long, stigma very small. Nutlets pitcherform, brown, 7 mm. long, 6–6.5 mm. broad, margins strongly inflexed, leaving a central aperture 2 mm. in diameter and radially slightly plicate, areola ovate, ca. 5 mm. long, dorsal middle area inside the pitcher smooth to tuberculate.

DISTRIBUTION: West Pakistan.

West Pakistan: MAKRAN DIST.: Inter Awaran et Turbat, 100–200 m., *Rechinger 27760* (W); ca. 20 km. west of Hushab, 100–200 m., rocky slope, sandy soil, *Lamond 391* (E); 17 miles from Hushab on Hushab-Turbat Road, *Kazmi 1147* (PES).

Rechinger & Riedl (*l. c.*) distinguished *Trichodesma longipedicellatum* from the other closely related species by these characters: "Species habitu elongato, caule flaccido, indumento brevi canescente, foliorum forma et petioli longitudine valde insignis." From a comparison of the descriptions of *T. longipedicellatum* and *T. stocksii* there appears little difference between the two species except that *T. longipedicellatum* is tall, robust with flaccid stems, and leaves with longer petioles, lanceolate to lanceolate-ovate, with acute apex. These characters are very variable, and even in the three collections cited above can hardly be relied upon. It appears that *T. longipedicellatum* is only a tall form of *T. stocksii*, growing under better conditions. On examination of the type of *T. stocksii* and other collections, *T. longipedicellatum* may prove to be only a variation of *T. stocksii*.

[*To be concluded*]



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COMPARATIVE ANATOMY OF ULMACEAE [1]

EDWARD M. SWEITZER

ULMACEAE IS A FAMILY of trees and shrubs of temperate and tropical regions. It is usually divided into two distinct subfamilies or tribes, the Ulmoideae or Ulmeae and the Celtidoideae or Celteae (as Celtideae). Leaves are always simple, often oblique at the base, and mostly alternate except in *Lozanella* where they are opposite. Stipules are caducous. Flowers are bisexual in *Ulmus* or functionally unisexual in most other genera. They are solitary, cymose, or in axillary fascicles. The perianth is made up of 4 to 8 connate or distinct sepals which are imbricate, campanulate, and persistent. A hypanthium is present in most genera of Ulmeae, but it is usually not apparent in Celteae. Stamens are differentiated into a bilocular anther supported by a filament; they are erect in the bud and inserted at the bases of the calyx lobes or opposite the sepals. The ovary is bicarpellate with 1 or 2 locules, and 2 styles stigmatose along their inner faces. The solitary ovule is anatropous and pendulous from near the apex of the ovary. The fruit is a winged samara with a straight embryo or a drupe with a curved embryo. Seeds lack endosperm.

A list of genera, their taxonomic characteristics, and geographical ranges is given in TABLE 1. Distribution maps for genera and species can be found in Bernard (1906). Also, a list of genera and the number of species considered by Hutchinson, by Engler and Prantl, and by Willis is given in TABLE 2. Hutchinson's (1967) listing and arrangement of genera will be used because it is the most complete modern listing for the family. (For TABLE 1, see p. 572.)

Palynologically the tribes Celteae and Ulmeae are more or less well defined (Erdtman, 1966). The pollen grains in Celteae are mostly 2- to 3-porate, suboblate to oblate-spheroidal, with an arcoid streaked sexine (some tegillate). Pollen grains of Ulmeae are 4- to 6-porate, colpate, or rupate, oblate to suboblate, with an arcoid streaked sexine (some tegillate).

Seeds of the Ulmeae are flattened with a straight embryo; fruits are usually samaras. Seeds of the Celteae are globose with the curved embryo surrounded by the bony endocarp of a drupe (McClure, 1957). Of the

[1] Contribution number 4367 of the Maryland Agricultural Experiment Station, Department of Botany, University of Maryland.

genera studied by Martin (1946), *Planera*, *Ulmus*, and *Zelkova* have investing embryos, *Celtis* has a folded embryo, and *Trema* a bent embryo.

Sax (1933) gives the haploid chromosome number for *Celtis*, *Holoptelea*, *Ulmus*, and *Zelkova* as 14. However, Darlington and Wylie (1955) list the haploid chromosome number for *Celtis* as 10, 11, 14.

TABLE 2. Genera and number of species in Ulmaceae*

GENUS	HUTCHINSON [a]	ENGLER & PRANTL [b]	WILLIS [c]
Ampelocera	9	2	4
Aphananthe	8	3–4	2
Barbeya	1		1
Celtis	150	60	41
Chaetachme	5	1	2
Chaetoptelea			1
Gironniera	30	7–8	5
Hemiptelea	1		1
Holoptelea	2	1	2
Lozanella	3		1
Mirandaceltis	1		
Parasponia	7	2	1
Phyllostylon	3	1	1
Plagioceltis			1
Planera	1	1	1
Pteroceltis	1	1	1
Trema	55	30	14
Ulmus	about 45	16	31
Zelkova	11	4	4

[a] 1967. [b] 1893. [c] 1966.

In the fossil record, the family is reported in strata identified from the Cretaceous (Berry, 1923; Andrews, 1961) and the following genera have been identified from the Tertiary: *Chaetoptelea*, *Celtis*, *Ulmus*, *Zelkova*, *Hemiptelea*, and *Pteroceltis* (Lesquereux, 1878, 1883; Andrews, 1961). Bernard (1906) stated that the Ulmaceae had a much wider distribution in the Tertiary than today, and that genera of Ulmaceae have been found as fossils in Greenland, Spitzbergen Island, northern Europe, Asia, and America. The present known distribution for each genus of Ulmaceae is given in TABLE 1. However, the genera may be arranged according to their presence in major geographical regions as follows: North America — *Celtis*, *Planera*, *Trema*, and *Ulmus*; Central and South America — *Ampelocera*, *Celtis*, *Chaetoptelea*, *Lozanella*, *Mirandaceltis*, *Phyllostylon*, *Plagioceltis*, and *Trema*; Europe — *Celtis*, *Ulmus*; Africa — *Celtis*, *Chaetachme*, *Holoptelea*, and *Trema*; Asia and the Pacific Islands — *Aphananthe*, *Celtis*, *Gironniera*, *Holoptelea*, *Parasponia*, *Pteroceltis*, *Trema*, and *Zelkova*. A recent paper by Elias (1970) discusses the taxonomy of *Ulmus*, *Celtis*, *Planera*, and *Trema* of the southeastern United States.

* For tables 1 and 4a, 4b, and 4c, see pages 572–584.

ECONOMIC USES AND IMPORTANCE

Commercially species of *Ulmus* and *Celtis* are valuable timber trees. According to Panshin *et al.* (1964), the wood is used for boxes and crates, veneers, and furniture because of its strength, excellent bending qualities, and great ability to withstand shock. "The murderous tomahawks of the Indians of North America were largely made of Elm wood" (Hutchinson, 1969). Species of *Zelkova* have been used in the making of small cabinets; *Phyllostylon brasiliensis* has been used for weaver's shuttles, scales, and piano keys (Desch, 1948). *Chaetoptelea* is used in Central America for railway crossties and for frames and wheels of vehicles; *Trema* wood has been used to some extent to make fine gunpowder charcoal (Record & Hess, 1943). *Aphananthe* and *Holoptelea* are employed for timbers in Asia and Africa (Metcalfe & Chalk, 1950).

Other uses made of the Ulmaceae include the following: *Trema* has been used to shade coffee and cocoa trees, and the fibers from bark have been used for cordage (Record & Hess, 1943). Fleshy drupaceous fruits of some species of *Celtis* are used for food; seeds of *Holoptelea integrifolia* are eaten in India. *Ulmus rubra* (slippery elm) and *Ulmus glabra* (European elm) bark has been used in folk medicine decoctions because of its high mucilage content (Kraemer, 1902; Hiscox, 1955); for example, elm tea, purported to be soothing in case of inflammation of the mucous membranes, is prepared by pouring one cup boiling water over two teaspoonfuls of powdered or whole slippery elm bark, cooling, straining, flavoring with lemon juice, and adding sugar to taste (Hiscox, 1955). The bark of *Holoptelea integrifolia* has been used as a remedy for rheumatism in India (Capoor, 1937). Elms have also been used locally as sacred symbols in France (Chevalier, 1942).

Many species of *Ulmus* have been used in the United States and elsewhere as street and park trees. Some species of *Celtis* and *Zelkova* are also used as ornamentals (Rehder, 1940). With the outbreak of Dutch elm disease in 1931 and its subsequent spread, many elm trees have died or are now dying. The organism *Ceratocystis ulmi* causes the disease on all native elms in the United States as well as on all European species; however, susceptibility to the disease varies. Symptoms include wilting and browning of leaves and subsequent defoliation; secondary xylem darkens with gummy accumulations. Some other diseases of *Ulmus* include black leaf spot caused by the fungus *Gnomonia ulmea* which infects young leaves that eventually become chlorotic and drop off; and dieback caused by the fungus *Dothiorella ulmi* which infects wounds causing canker formation. Phloem necrosis caused by the virus *Morsus ulmi* usually results in the death of the tree; verticillium wilt caused by the fungus *Verticillium alboatrum* results in wilted and chlorotic leaves; wetwood caused by the bacterium *Erwinia nimipressuralis* may result in wilting and defoliation, among other symptoms. *Celtis occidentalis* (hackberry) may have broom-like growths on branches, a condition called witches'-broom. The fungus *Sphaerotheca phytophylla* and species of the gall mite *Eriophyes* are

usually found in the buds, and the resulting branches that develop are dwarfed and clustered (Linder, 1931; Pirone, *et al.*, 1960; J. C. Walker, 1969; Nichols, 1970).

TAXONOMY

The family name, Ulmaceae, can be traced back to Mirbel (1815), at which time the family included only *Ulmus* and *Celtis*. Dulac (1867) used Samaraceae as the family name. Link (1831) proposed splitting Ulmaceae into two families: Ulmaceae, composed of *Ulmus* and related genera, and Celtaceae (as Celtidaceae), comprising *Celtis* and related genera.

For the most part, the family Ulmaceae has been considered a natural taxon. There has been much uniformity both in the generic content and in its placement with relationship to other families. Planchon (1873) recognized the order (family) Ulmaceae which he divided into two suborders (subfamilies): Ulmeae containing *Ulmus*, *Holoptelea*, *Hemiptelea*, *Zelkova*, and *Planera* and Celteae (as Celtideae) with *Celtis*, *Parasponia*, *Sponia*, *Gironniera*, *Aphananthe*, and *Chaetachme*. Endlicher (1837) listed the orders (families) Ulmaceae, with *Ulmus* and *Planera* and Celteae (as Celtideae) containing *Celtis*, *Sponia*, and *Mertensia*, in his class Juliflorae. Bentham and Hooker (1862) arranged the tribes Ulmeae, Celtideae, Cannabineae, Moreae, Artocarpeae, Conocephaleae, Urticeae, and Thelygoneae in the family Urticaceae. Lindley's (1853) alliance (our present day order) Urticales included Urticaceae, Cannabaceae (as Cannabinaceae), Moraceae, Artocarpaceae, etc.; however, he placed the Ulmaceae, including *Celtis* and *Ulmus*, in the alliance Rhamnales along with Aquilariaceae, Rhamnaceae, Hippocrateaceae, Celastraceae, Sapotaceae, and other families.

Toward the end of the nineteenth century many authors, dissatisfied with previous systems of classification, attempted to show more natural relationships in their taxonomic treatments. However, the position and content of the Ulmaceae changed very little. Baillon (1880) defined an expanded family, Ulmaceae, which included the series Ulmeae (*Celtis*, *Ulmus*, and other genera), Moreae, Artocarpeae, and Cannabineae. Eichler (1878) assigned the Ulmaceae (*Ulmus*, *Celtis*) to the taxon Urticinae which included Urticaceae, Moraceae, Artocarpaceae, Platanaceae, and Ceratophyllaceae.

Engler and Prantl (1893) placed the Ulmaceae in the Urticales along with the Rhoipteleaceae, Eucommiaceae, Moraceae, and Urticaceae. They divided Ulmaceae into two subfamilies: Ulmoideae, containing *Phyllostylon*, *Holoptelea*, *Ulmus*, and *Planera*; Celtidoideae including *Celtis*, *Pteroceltis*, *Ampelocera*, *Zelkova*, *Trema*, *Parasponia*, *Aphananthe*, *Gironniera*, and *Chaetachme*. The Urticales was placed in the subclass Archichlamydeae (Apetalae and Choripetalae). Engler and Prantl had the Urticales arising independently from the hypothetical Protangiospermae: Melchior, in the 1964 "Syllabus," followed the same pattern.

Hallier (1912) derived the Terebinthales from the Ranales and had the Terebinthaceae giving rise to the Urticaceae (in the broad sense of Bentham and Hooker, 1862). Bessey (1915) placed the Ulmaceae (*Ulmus*, *Celtis*, *Zelkova*, *Planera*) along with the Moraceae and Urticaceae in the Malvales. He derived the Malvales from the Ranales. Wettstein (1935) placed the Ulmaceae, Moraceae, Cannabaceae, Eucommiaceae, Rhoipteleaceae, and Urticaceae in the Urticales. He traced this order from the same gymnospermous line which produced Fagales and Juglandales and thought that the Hamamelidales arose close to the Urticales. Rendle (1938) placed the Ulmaceae (Ulmeae and Celteae (as Celtideae), Urticaceae, and Moraceae in the order Urticiflorae, but the overall position of the order is similar to that proposed by Engler and Prantl.

Gundersen (1950) put Ulmaceae, Eucommiaceae, Moraceae, and Urticaceae in the Urticales and placed the order in his "Ulmus group" which included Proteales, Santalales, Balanopsidales, Fagales, Leitneriales, and Casuarinales. He derived this group from his "Rosa group" (Rosales, Hamamelidales, Thymelaeales, and Myrtales) which he in turn traced from the complex containing Magnoliales, Ranales, and Piperales. Gundersen considered his "Ulmus group" to be, probably, an unnatural taxon.

Hutchinson (1967) divided the Ulmaceae into two tribes: Ulmeae, containing *Phyllostylon*, *Holoptelea*, *Planera*, and *Ulmus*, and Celteae (as Celtideae), with *Celtis*, *Pteroceltis*, *Ampelocera*, *Zelkova*, *Hemiptelea*, *Trema*, *Parasponia*, *Aphananthe*, *Mirandaceltis*, *Gironniera*, *Chaetachme*, and *Lozanella*. He included the family in the Urticales along with Cannabaceae (as Cannabiaceae), Moraceae, Urticaceae, Barbeyaceae, and Eucommiaceae. Hutchinson (1969) indicated that ". . . the above families . . . have a quite lengthy pedigree, maybe as follows: Magnoliales → Dilleniales → Rosales → Hamamelidales → Fagales → Urticales climax family Urticaceae (mostly herbaceous)."

Thorne (1968) placed the Ulmaceae, with subfamilies Ulmoideae and Celtidoideae, in Urticales under the superorder Malviiflorae (Malvales, Rhamnales, Euphorbiales, Solanales, Campanulales). Cronquist (1968), likewise, put Ulmaceae in the order Urticales along with Barbeyaceae, Moraceae, Cannabaceae, and Urticaceae. He placed the order in the subclass Hamamelidae which included Trochodendrales, Hamamelidales, Eucommiales, Leitneriales, Juglandales, Myricales, Fagales, and Casuarinales. The Hamamelidae have arisen from the Magnoliidae (Magnoliales, Piperales, Aristolochiales, Nymphaeales, Ranunculales, Papaverales). Takhtajan (1969) placed Ulmaceae, Moraceae, Cannabaceae, and Urticaceae in the Urticales which he has connected to the Hamamelidales and which is perhaps derived from it. The Hamamelidales are derived directly from the Magnoliales through the Trochodendrales.

There recently has been a renewed suggestion that the Ulmaceae be split into two families, as formerly suggested by Link (1831). Grudzinskaya (1967) states:

> In its main diagnostic characters the subfamily *Celtidoideae* is more similar to the family *Moraceae* than to *Ulmoideae*; for this reason it should be ex-

cluded from the family *Ulmaceae*. The distinct features isolating *Celtidoideae* from the closely allied families justifies the classification of this subfamily as a separate family *Celtidaceae* Link. The genera *Zelkova* and *Hemiptelea* should be excluded from *Celtidaceae* because their morphological characters and genetic affinities indicate that they belong to *Ulmaceae* s. str. Thus, the generic composition of the two families is as follows — Ulmaceae: *Ulmus*, *Holoptelea*, *Hemiptelea*, *Zelkova*, *Planera*, *Phyllostylon*; Celtidaceae: *Celtis*, *Pteroceltis*, *Trema*, *Parasponia*, *Lozanella*, *Aphananthe*, *Gironniera*, *Chaetachme*, *Ampelocera*.

Since there is general acceptance that the Ranalian complex is primitive in the dicotyledons, there has been little disagreement as to the position of the Ulmaceae in the order Urticales. Cronquist (1968) asserts that "The naturalness of the order Urticales is not in dispute." The only major point of disagreement among the four leading contemporary plant phylogenists, Cronquist, Hutchinson, Takhtajan, and Thorne, relates to the position of Urticales. In Thorne's treatment it is included with Malvales and related taxa, whereas the others place it close to the Hamamelidales and related taxa.

Other minor points of variance concern an assessment of the tribes of Ulmaceae and the status of some genera. Grudzinskaya is the only present-day taxonomist I know who supports the formation of two distinct families from the two subgroups within Ulmaceae. Genera whose position within the Ulmaceae has been questioned or whose status may merit separate taxonomic integrity as a family are *Barbeya*, *Chaetoptelea*, *Mirandaceltis*, *Gironniera*, and *Plagioceltis*. In a recent study, Dickison and Sweitzer (1970) supported placing *Barbeya* in a separate family, and keeping it in the Urticales. The genus *Chaetoptelea* has been assigned by most taxonomists to the genus *Ulmus*. However, there is some evidence from paleobotanical studies and from external morphological investigations indicating that *Chaetoptelea* may be recognizable as a distinct genus. *Mirandaceltis* is a monotypic genus proposed by Sharp (1958), which other taxonomists have retained in the genus *Celtis*. The genus *Plagioceltis* was described by Mildbraed (1937) ex Baehni in Macbride's *Flora of Peru*. However, little is known about the genus other than from specimens collected by Ruiz and Pavón. The holotype is in Madrid; Ruiz and Pavón did not note the collection site. Therefore, I was unsuccessful in obtaining anatomical material for study.

ANATOMICAL REVIEW

There has been no comprehensive anatomical study of secondary xylem of Ulmaceae although there are several minor studies, the most extensive being the work of Tippo (1938) for which he examined nine genera and 29 species. Grumbles (1914) studied the comparative wood anatomy of four oriental species of *Celtis*, and Cox (1941) examined the wood of five American species of the same genus. The wood anatomy of *Ampelo-*

cera glabra was investigated by Milanez (1937); Record and Garratt (1925) and Desch (1948) described the secondary xylem anatomy of *Phyllostylon brasiliensis*. Record and Mell (1924) and Record and Hess (1943) described some features of the wood anatomy of several genera, including *Ampelocera*, *Celtis*, *Chaetoptelea*, *Phyllostylon*, *Planera*, *Trema*, *Ulmus*. In a work entitled "Phylogénie des Ulmacées," Houlbert (1899) discussed the need of using "echantillons d'age avancé" in phylogenetic studies based on wood anatomy He studied a complete range of *Ulmus* woods of various ages and attempted to correlate yearly differences in *Ulmus* with mature wood characters of related genera to show evolutionary development. Major summary works dealing with secondary xylem anatomy and general anatomy of some genera of Ulmaceae include those of DeBary (1884), Solereder (1908), and of Metcalfe and Chalk (1950).

Works pertaining to aspects of anatomy other than wood structure vary in their completeness. A study of the leaf anatomy of 14 genera and 80 species of the Ulmaceae was carried out by Priemer (1893). Leaf ontogeny of *Zelkova serrata* was investigated by Soma (1965). Gardiner (1965) attempted to correlate leaf anatomy and geographic distribution in *Trema*. Petiolar anatomy of *Celtis* and several other urticalean genera was studied by Sarabhai and Saxena (1961).

Bechtel (1921) published work on the floral anatomy of the Urticales, including Ulmaceae (five species of *Ulmus*, one species of *Celtis*). Several studies have been made of megasporogenesis, microsporogenesis, and embryology; for example that of Shattuck (1905) on *Ulmus americana*; of Capoor (1937) on *Holoptelea integrifolia*; of Eckardt (1937) on *Ulmus montana*, *Celtis tournefortii* and genera of related pseudomonomerous families; and of R. I. Walker (1938, 1949) on various species of *Ulmus*. General summary works dealing with embryology which include some genera of the Ulmaceae are listed in the work of Maheshwari (1950), of Eames (1961), and of Davis (1966). The embryo sac of *Celtis* is of the Polygonum type and that of *Ulmus* of the Adoxa or Drusa type.

The secondary phloem anatomy of *Ulmus*, *Celtis*, *Gironniera*, *Trema*, and *Zelkova* was investigated by Zahur (1959). Sieve tube ontogeny in *Ulmus americana* has been investigated with the light microscope (Evert *et al.*, 1969) and with the electron microscope (Evert & Deshpande, 1969).

SECRETIONS AND CHEMOTAXONOMY

Various intracellular substances, such as silica, calcium carbonate, and mucilage, have been reported to occur in different organs, tissues, and cells of most ulmaceous genera. Amos (1952) reported the presence of vitreous silica in vessels and parenchyma cells of the secondary xylem of *Gironniera*. He also stated that wood specimens of *Aphananthe*, *Celtis*, *Holoptelea*, *Phyllostylon*, *Trema*, *Ulmus*, and *Zelkova* showed no evidence of silica formation. Priemer (1893) reported that the leaf epidermis and hairs of the species of *Zelkova*, *Aphananthe*, *Ulmus*, *Celtis*, and *Trema*

he investigated were silicified. Various techniques for analysis of silica are contained in Satake (1931), Uber (1940), Amos (1952), Lanning, *et al.* (1958), and Jones and Handreck (1967). A recent review of silicon physiology can be found in Lewin and Reimann (1969). Actual chemical analyses for the presence of silica were beyond the scope of this investigation.

The presence of calcium carbonate in old vessels of wood was reported in Haberlandt (1928) for *Ulmus glabra* and *Celtis orientalis*. Secondary xylem deposits of calcium carbonate were noted in several species of *Ulmus*, *Celtis*, and *Phyllostylon* by Record (1927). Priemer (1893) reported the presence of calcium carbonate in the form of cystoliths in the leaves of several ulmaceous genera. Satake (1931) found calcium carbonate cystoliths in *Celtis* and *Trema* leaves. Pireyre (1961) discussed cystoliths from morphologic, histologic, and physiologic bases in two species of *Celtis* as well as other non-ulmaceous genera. Metcalfe and Chalk (1950) listed various genera reported to have calcium carbonate deposits. Techniques for the determination of calcium carbonate can be found in Satake (1931), Scott (1946), and Pireyre (1961). Chemical analyses of calcium carbonate were beyond the scope of this study.

Mucilage has been identified in the past by its viscous appearance in sectioned tissues, the chemical nature of this substance has been little investigated and the microscopist has had to rely on nonspecific visual observations rather than specific histochemical tests. The literature is replete with reports on mucilaginous and gummy materials in the leaves, bark, and roots of several ulmaceous genera and species, especially *Ulmus rubra* and *U. glabra* bark which has a high mucilage content. Lawrence (1951), Metcalfe and Chalk (1950), and Hutchinson (1969).

Smith and Montgomery (1959) discussed plant gum and mucilage chemistry. Practical histochemical implications of their work are yet to be realized, but because of the apparent ubiquitous occurrence of these or related substances in Ulmaceae, a brief consideration of gum and mucilage chemistry is perhaps in order at this point. Mucilages are products of normal plant metabolism and may serve as food reserves. There is no clear chemical distinction between gums and mucilages and both are complex polysaccharides. The complexity of these compounds is due to the type of linkage and component building units; mucilage bodies result from regularly spaced side chains, whereas gums have irregular substitutions. Mucilages give rise to thick gels; gums dissolve in water and give clear solutions with adhesive properties. TABLE 3 shows Smith and Montgomery's conceptual classification of gums and mucilages. The hydrolysis products of *Ulmus rubra* (as *U. fulva*) mucilage are D-galactose, 3-O-methyl-D-galactose, L-rhamnose, and D-galacturonic acid (Robinson, 1963).

In the only comparative chemotaxonomic study encountered, Lebreton (1965) discussed the relationships within the Urticales based on flavonoids. He specifically analyzed species of *Celtis* and *Ulmus* and his results are noted in the DISCUSSION.

TABLE 3. Classification of gums and mucilages[a]

GROUP I		GROUP II
Acidic gums and mucilages containing:		Neutral gums and mucilages containing:
Acid components	*Neutral components*	
L-guluronic acid	Hexoses	Hexoses
D-glucuronic acid	Pentoses	6-Deoxyhexoses
D-galacturonic acid	6-Deoxyhexoses	Pentoses
Sulfate groups	Sugar alcohols	Sugar alcohols
Phosphate groups	Ethers of all of the above	Ethers of all of the above
Ethers of all of the above		

[a] From Smith & Montgomery (1959).

PROBLEMS AND OBJECTIVES

A study of the wood and leaf anatomy should provide additional information for phylogenetic studies of Ulmaceae and at the same time help to clarify ordinal relationships and intrafamilial systematic problems. The latter include the taxonomic status of the two major subdivisions of Ulmaceae and of the genera *Chaetoptelea*, *Mirandaceltis*, and *Gironniera*. Anatomical data will be correlated with other pertinent information to provide a firmer basis for an interpretive discussion of the affinities and composition of Ulmaceae.

In addition, leaf and wood anatomy can be used in the identification of species from local floras, which might be useful in the identification of commercially important ulmaceous timbers, possible drug plants, and potential ornamentals. A knowledge of wood anatomy is imperative in some aspects of forensic botany. *Ulmus* species and varieties vary in their susceptibility to Dutch elm disease and elm phloem necrosis. These are, at least in part, diseases of the vascular system, and susceptibility and resistance may be related partially to differences in the vascular tissue, which a thorough anatomical study might reveal, making possible a more effective breeding program for disease resistance.

MATERIALS AND METHODS

For the most part, the terminology of xylem anatomy used here is in agreement with that suggested by the Committee on Nomenclature of the International Association of Wood Anatomists (1957). Terms used to describe overall venation patterns in leaves are taken from von Ettingshausen (1861). Additional terms conform to current usage and deviation from such usage is explained where employed in the text.

Standard techniques were used in preparing specimens for observation. Dried wood specimens were hydrated in boiling water, dehydrated in ethyl alcohol, and embedded in celloidin. Wood specimens preserved in

formalin-acetic acid-alcohol (FAA) were dehydrated and embedded in celloidin. Transverse, radial, and tangential sections were cut on a sliding microtome, stained with Heidenhain's iron-alum haematoxylin, and counterstained with safranin. Wood macerations were prepared using Jeffrey's fluid, washed in water, stained with safranin, and dehydrated with tertiary-butyl alcohol. Sections and macerations were mounted in Canada balsam.

Leaves preserved in FAA and dried leaves from herbarium specimens were used in this study. All dried leaves were first hydrated in boiling water; clearings of leaves were made following Arnott's (1959) technique using 5 percent sodium hydroxide, followed by a water wash, and treatment with a saturated aqueous solution of chloral hydrate. Leaves were then washed with water, stained with aqueous safranin, dehydrated in ethyl alcohol, and mounted in Canada balsam. Transverse and paradermal sections of leaves were embedded in paraffin and cut on a rotary microtome. Sectioned leaves were stained with safranin and fast green, cleared in clove oil and toluene, and mounted in Canada balsam.

Pore distributions expressed as percentages were obtained by counting 10 microscope fields from the transverse sections. Tangential pore diameters, vessel element lengths, and imperforate tracheary element lengths are based on 50 measurements each. Tangential pore diameters were measured only in the last completely formed growth ring. For all ring porous specimens, 25 tangential pore diameters were measured from the first formed portion of the growth ring and 25 from the last formed portion of the growth ring. Vessel elements were measured from tip to tip to obtain the length. From the leaf clearings the approximate frequency of cystoliths was obtained by counting the cystoliths contained in a one millimeter square area of leaf surface.

About 25 percent of the microscope slides of wood specimens employed in this study were prepared in the laboratory of Dr. Oswald Tippo. Preparation of these specimens was probably the same as employed here except for softening in hydrofluoric acid for the hardest specimens. Lists of all specimens used in this study are given in TABLES 4a, 4b, and 4c. Identifications used are those originally accompanying specimens, except that nomenclature of cultivated species follows Rehder (1940) and that of species indigenous to the United States follows Little (1953).

Microchemical tests were not performed to determine the presence of silica, mucilage, or calcium carbonate, each of which has been reported previously in cells and tissues of Ulmaceae. When these terms are used they are in general agreement with reports from the literature; silica has a glass-like appearance, mucilage is viscous to frothy in texture, and calcium carbonate stains to varying degrees with safranin and fast green. (For TABLES 4a, 4b, and 4c, see pages 574–584.)

RESULTS

The sequence of genera for the anatomical descriptions of leaf and wood

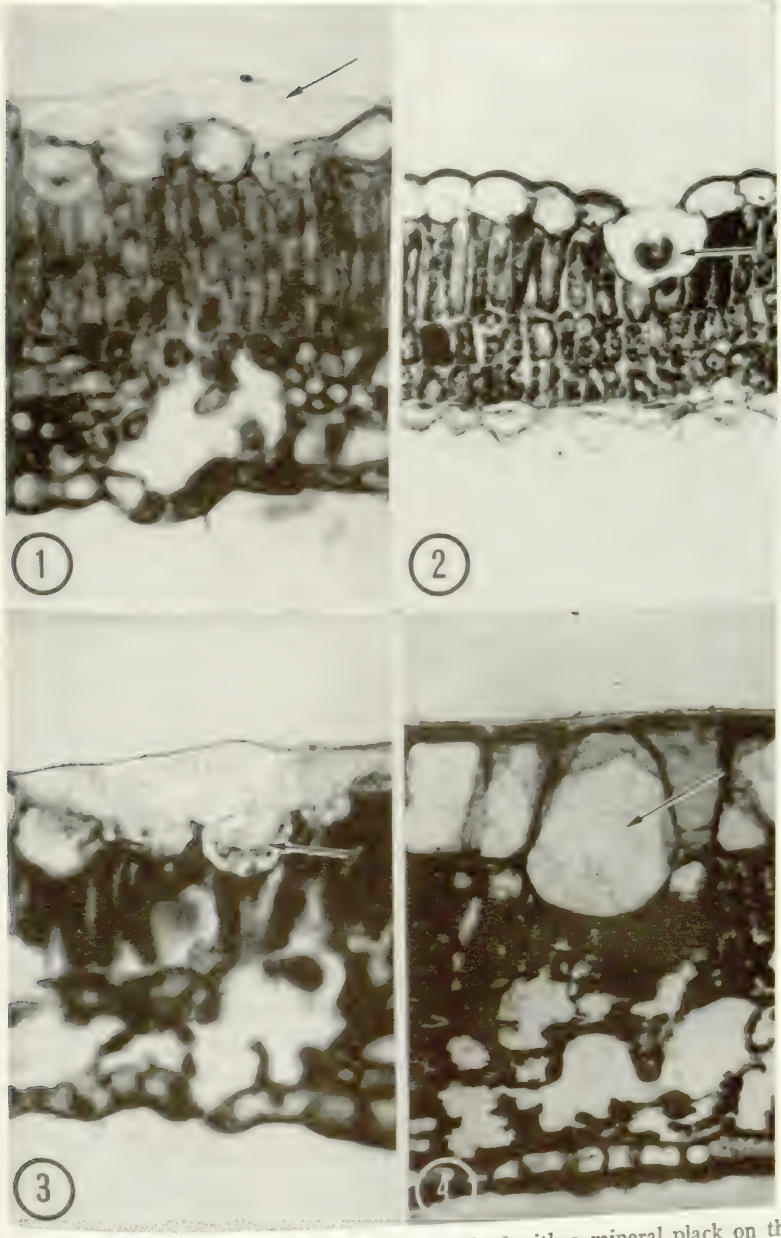

FIGURE 1. *Zelkova sinica*. Cross section of leaf with a mineral plack on the upper epidermis. × 320. 2. *Celtis tournefortii*. Cross section of leaf with a cystolith in the upper epidermis and a compact spongy mesophyll. × 320. 3. *Ulmus parvifolia*. Cross section of leaf with a pegless cystolith in an upper epidermal cell below a mineral plack. × 320. 4. *Chaetachme microcarpa*. Cross section of leaf with an enlarged upper epidermal cell containing frothy mucilage, × 320.

follows Hutchinson (1967), except for *Chaetoptelea* which he included in *Ulmus*.

In the generic descriptions which follow, the number of species, in parentheses, is followed by the number of specimens if there were more specimens than species examined.

LEAF

Since several descriptive terms refer to structures and substances which are not widespread, their usage in this paper is explained here. Silica or siliceous refers to any material which is glass-like in appearance; the term mineral plack refers to the silica and/or calcium carbonate covering an epidermal area composed of several cells, i.e., both on the surface and between the cells (FIGURE 1).

Cystolith refers to an anisotropic crystalline concretion of both calcium carbonate and silica (Pireyre, 1961) of varying shapes and colors which may or may not have a peg. A peg is a cellulosic extension of the cell wall on which the crystalline material is deposited. Pegged cystoliths usually become stained (safranin and fast green), whereas the pegless cystoliths remain glassy to white-opaque even after staining (FIGURES 2, 3).

Mucilage refers to cellular contents which appear viscous to frothy in texture and vary in color from gray-green to pink when stained with safranin and fast green (FIGURE 4).

The terms loose and compact, as applied to the spongy mesophyll, refer to the relative amount of intercellular space. Also, a loose spongy mesophyll has relatively fewer cells per unit volume than a compact spongy mesophyll (FIGURES 5, 2).

The following leaf anatomical features occur throughout the entire family with exceptions listed: leaves are dorsiventral, the cuticle is less than five microns thick, the stomatal apparatus is anomocytic, and guard cells are elongate-reniform (FIGURE 6). Stomates are found only on the lower epidermis. Both upper and lower epidermis are uniseriate, except in *Trema amboinensis* and *T. orientalis* where the upper epidermis is 2 or 3 layers thick. The lower epidermis is papillate beneath major veins in the following genera: *Phyllostylon*, *Planera*, *Ulmus*, *Zelkova*, *Hemiptelea*, *Parasponia*, *Mirandaceltis*, *Gironniera*, and *Lozanella*. In most species of *Celtis* the entire lower epidermis is papillate. A parenchymatous bundle sheath surrounds both major and minor veins; however, surrounding some of the larger veins, there are also gelatinous thick-walled parenchyma cells.

Unicellular trichomes have a bulbous base (FIGURE 7) and occur on both the upper and lower epidermis. The walls are usually impregnated with silica. Multicellular hairs usually found on both leaf surfaces are of three basic types: the first found in some species of *Phyllostylon*, *Planera*, *Ulmus*, *Chaetoptelea*, *Celtis*, *Ampelocera*, *Zelkova*, *Hemiptelea*, *Trema*, *Aphananthe*, and *Lozanella* comprises a uniseriate linear row of

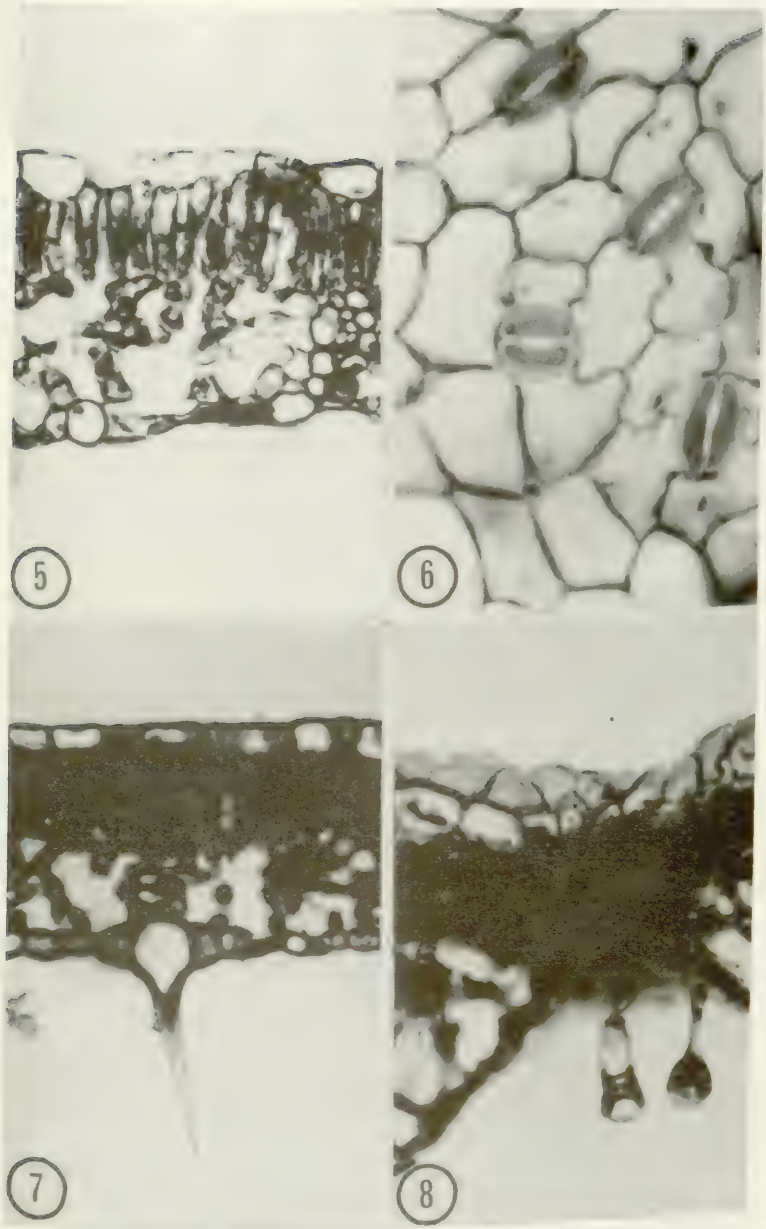

FIGURE 5. *Ulmus glabra*. Cross section of leaf with a loose spongy mesophyll. × 320. 6. *Pteroceltis tatarinowii*. Paradermal section of leaf with an anomocytic stomatal apparatus and elongate reniform guard cells. × 400. 7, *Ulmus glabra*. Cross section of leaf with a bulbous-based unicellular hair, × 220. 8, *Ulmus rubra*. Cross section of leaf with two uniseriate multicellular trichomes, × 430.

cells (3–8) with the terminal cell and sometimes stalk cells being glandular, that is, containing dark staining material (FIGURE 8) and in addition some of the hairs are biseriate throughout their length in *Trema*. The second type has a uniseriate linear stalk of 3 to 8 cells but a multicellular glandular head of 2 to 4 cells and is found in some species of *Ulmus*, *Celtis*, *Ampelocera*, *Parasponia*, *Gironniera*, and *Lozanella* (FIGURE 9). The third type has a multicellular stalk with a single enlarged terminal cell in some species of *Ulmus* and *Trema* (FIGURE 10). Trichomes are usually associated with veins

Phyllostylon (2). Multicellular hairs found only on the lower epidermis; overall venation pattern brochidodromous, and terminal tracheids in areoles are surrounded by a parenchyma sheath. Leaf margin is serrate in *Phyllostylon rhamnoides* and entire in *P. brasiliensis*; palisade mesophyll is 1 to 4 cells deep, the spongy mesophyll is compact; bundle sheath extensions not well developed in *P. brasiliensis* but conspicuous in *P. rhamnoides*.

Cystoliths present in enlarged cells of both upper and lower epidermis in *P. rhamnoides*. There are about 60 per mm.^{2} in the upper epidermis and 40 per mm.^{2} in the lower epidermis. In *P. brasiliensis* they are only in the lower epidermis and number about 100 per mm.^{2} Druses are found in the mesophyll and phloem of both species; in addition, *P. rhamnoides* has prismatic crystals in the bundle sheath and phloem and styloids in all living tissues.

Holoptelea (1). Leaf margins are entire, the overall venation pattern is brochidodromous. In the areole, the veins terminate as individual tracheary elements without a sheath (FIGURE 11). A uniseriate palisade layer and a medium compact spongy layer are present. Chlorenchymatous bundle sheath present around both major and minor veins; chlorenchymatous bundle sheath extensions on both sides of major veins.

Cystoliths present in enlarged cells of the lower epidermis and in bases of unicellular hairs. Cystoliths approximately 30 per mm.^{2}; druses occurring in cells of upper and lower epidermis, mesophyll, and phloem.

Planera (1). Multicellular hairs on the lower epidermis only, leaf margins serrate, the overall venation pattern is "simply" craspedodromous; veins terminating in areoles as individual tracheary elements without a sheath; mesophyll composed of a palisade layer 1 or 2 cells thick and a loose spongy layer; a bundle sheath extension present on both sides of major veins; mineral placks present on upper epidermis; druses present in the mesophyll; styloids in cells of both mesophyll and epidermis.

Ulmus (15, 27). Multicellular trichomes found in all species except *U. americana*, *U. crassifolia*, *U. glabra*, *U. minor*, *U. laevis*, *U. parvifolia*, and *U. thomasii*. Leaves oblique at base, margins varying from simply to

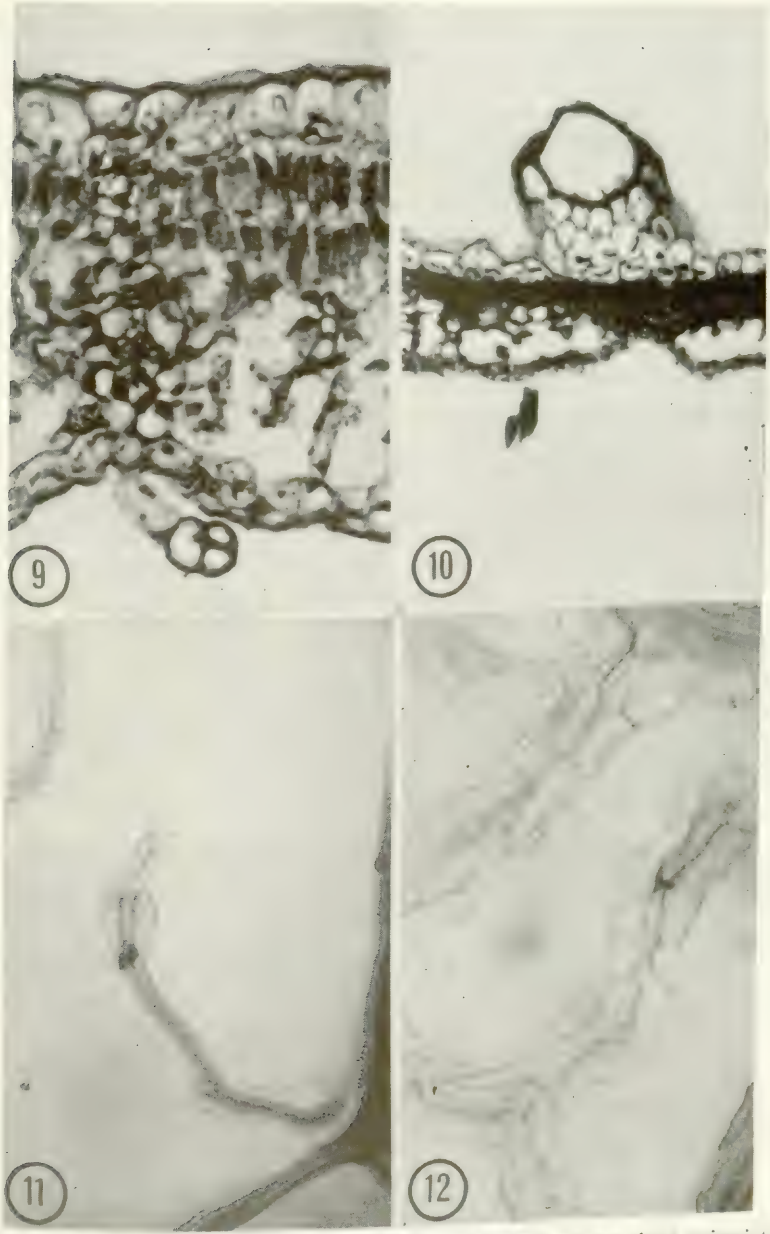

FIGURE 9, *Ulmus carpinifolia*. Cross section of leaf showing a short uniseriate stalked trichome with a multicellular head. × 400. 10, *Ulmus rubra*. Cross section of leaf with a multiseriate stalked hair with an enlarged terminal cell, × 250. 11. *Holoptelea integrifolia*. Clearing of leaf to show tracheary elements in the areole without bundle sheaths. × 300. 12, *Ulmus americana*. Clearing of leaf to show tracheary elements in the areole with a bundle sheath, × 300.

triply serrate; venation pattern is "simply" craspedodromous; terminal vein endings enclosed by a conspicuous parenchyma sheath within the areole (FIGURE 12); palisade mesophyll 1 to 4-seriate; the spongy mesophyll loose; bundle sheath extensions present on major veins.

Enlarged mucilage-containing cells occur in both upper and lower epidermal layers; mineral placks present in the upper epidermis. In several species, e.g., *U. parvifolia* and *U. glabra*, some upper epidermal cells below placks contain pegless cystoliths. Druses mostly in mesophyll and bundle sheath cells and to a lesser extent in cells of phloem and bundle sheath extensions; prismatic crystals commonly in the bundle sheath and phloem cells and to a lesser extent in cells of bundle sheath extensions; styloids present in cells of mesophyll and epidermis; mucilage-filled lacunae, resulting from cell disintegration found below midrib and other large veins in most species (FIGURE 13); these lacunae may be traumatic in origin.

Chaetoptelea (1). Leaf margin serrate, overall venation pattern is "simply" craspedodromous; in the areole, terminal tracheary elements are surrounded by a bundle sheath; mesophyll comprising a palisade layer of 1 or 2 cells and a loose spongy layer; bundle sheath extensions present only on major veins.

Mineral placks found covering clusters of cells in upper and lower epidermis; druses found in cells of mesophyll, bundle sheath, and bundle sheath extensions; prismatic crystals present in phloem, bundle sheath, and bundle sheath extension cells; styloids occurring in mesophyll and epidermal cells.

Celtis (17, 28). Multicellular trichomes occur only in *Celtis iguanaea*, *C. pubescens*, *C. reticulata*, and *C. sinensis*. The leaf margins vary from entire in *C. occidentalis* and *C. schippii* to serrate in *C. triflora* and *C. pumila*. Species with serrate margins have teeth mostly from the middle of the leaf to the tip. *Celtis laevigata*, *C. jessoensis*, and *C. reticulata* have oblique leaf bases. Overall venation pattern brochidodromous except in *C. philippinensis* where it is "perfect" actinodromous. Most species lack a parenchyma sheath around the terminal tracheary elements of the areole, except *C. caudata*, *C. jessoensis*, *C. philippinensis*, *C. schippii*, and *C. spinosa*. Palisade mesophyll has 1 to 3 layers, the spongy mesophyll is compact except in *C. pallida* where it is loose; bundle sheath extensions present on major veins except in *C. iguanaea* and *C. spinosa*.

Cuticular ridges on upper and lower epidermis of *C. occidentalis*, *C. pumila*, and *C. tournefortii*, and on lower epidermis only of *C. jessoensis*, *C. laevigata*, *C. reticulata*, *C. sinensis*, and *C. tenuifolia*. Upper epidermal anticlinal walls sinuous in most species; outer periclinal walls of upper epidermis thickened in *C. laevigata*, *C. pallida*, *C. reticulata*, and *C. tournefortii*.

Pegged cystoliths present in enlarged upper and lower epidermal cells

and in unicellular hairs, these present only in the upper epidermis of *C. laevigata*, *C. occidentalis*, *C. philippinensis*, *C. pubescens*, *C. pumila*, *C. sinensis*, *C. tenuifolia*, and *C. tournefortii*, and in the upper and lower epidermis of all other species. Pegless cystoliths found in enlarged upper and lower epidermal cells of *C. schippii*; the number of cystoliths per mm.^{2} ranging from 40 to 148 in the upper epidermis and from 0 to 48 in the lower epidermis.

Prismatic crystals present in bundle sheaths of most specimens and in phloem of *C. caudata*, *C. iguanaea*, and *C. spinosa*; no prismatic crystals present in *C. pallida*, *C. schippii*, and *C. trinervia*; styloids found in living cells of all tissues of *C. pallida*; mucilage not found in *C. iguanaea*, *C. spinosa*, or *C. trinervia*.

Pteroceltis (1, 2). Leaf margin serrate and overall venation pattern brochidodromous; terminal tracheary elements surrounded by a sheath of round to oval cells; mesophyll divided into a palisade layer (1 or 2-seriate) and a loose spongy layer; major veins with bundle sheath extensions.

Pegged and unpegged cystoliths occurring in enlarged cells and hairs of the upper and lower epidermis; cystoliths in distinctive clusters of 20 (±) cells, usually surrounding a trichome; druses found in cells of the mesophyll, bundle sheath, bundle sheath extension, and phloem; styloids present in the mesophyll.

Ampelocera (3). Multicellular hairs occurring on the lower epidermis of *Ampelocera cubensis*; short stalked hairs with a glandular, multicellular capitate head occurring in indentations of upper and lower epidermis of *A. hottlei* (FIGURE 14). No multicellular hairs found on *A. edentula*.

Leaf margin entire and leaf base slightly oblique; overall venation pattern brochidodromous; terminal tracheary elements having a sheath in *A. hottlei*, but not in *A. cubensis* or in *A. edentula*. Palisade mesophyll with 1 or 2 layers, the spongy mesophyll varying from loose in *A. hottlei* to compact in *A. cubensis*; bundle sheath extensions found only in *A. cubensis*.

Pegged cystoliths in enlarged cells of the upper epidermis of all species (1 to 40 per mm.^{2}) and in the lower epidermis of *A. hottlei* (12 per mm.^{2}); druses in the mesophyll, bundle sheath, and phloem of *A. hottlei*; prismatic crystals in bundle sheaths of *A. edentula* and *A. hottlei* and also in phloem of the latter; styloids in living cells of all tissues in *A. cubensis*.

Zelkova (3, 4). Leaves with an oblique base and serrate margins; overall venation pattern "simply" craspedodromous and tracheary elements in the areole surrounded by a parenchyma sheath; mesophyll with 1 or 2 palisade layers and a loose spongy layer; major veins with bundle sheath extensions.

Pegless cystoliths in upper and lower epidermal cells; mineral placks

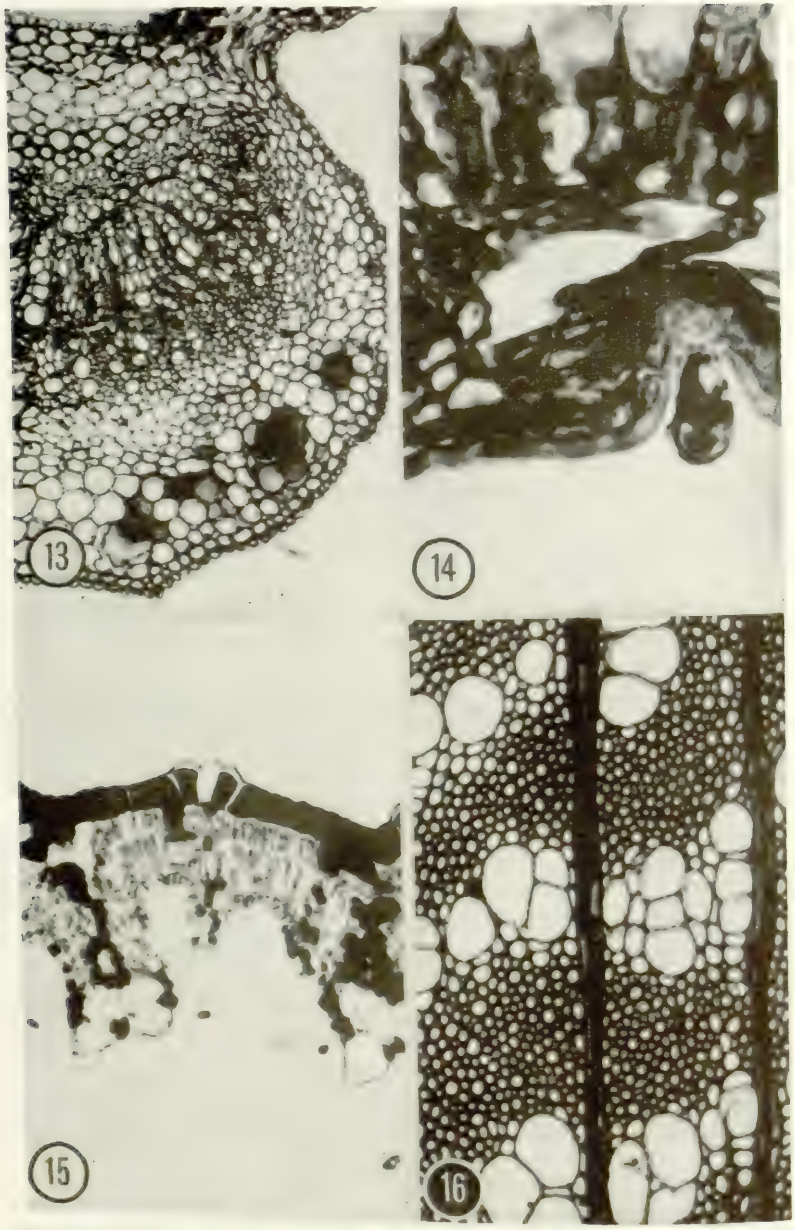

FIGURE 13, *Ulmus rubra*. Cross section of midrib of a leaf showing mucilage-filled cavities. × 140. 14, *Ampelocera hottlei*. Cross section of leaf with a multicellular hair in an indentation of the lower epidermis, × 450. 15, *Trema lamarckiana*. Cross section of leaf illustrating the uneven lower epidermis. × 110. 16. *Ulmus americana*. Transverse wood section illustrating the tangential (wavy) pore arrangement, × 120.

on the upper epidermis; prismatic crystals in the phloem, bundle sheath, and bundle sheath extensions; styloids in all living tissues of *Zelkova carpinifolia* and *Z. sinica*.

Hemiptelea (1, 2). Multicellular hairs on the lower epidermis; leaf margins serrate, the overall venation pattern "simply" craspedodromous; terminal tracheary elements in the areole surrounded by a sheath; two or three palisade layers and a loose to medium compact spongy layer; bundle sheath extensions on upper and lower sides of major veins.

Pegged cystoliths in upper and lower epidermis; in upper epidermis cystoliths arranged in groups with a unicellular hair in the center (32 to 120 cystoliths per mm.^{2}); cystolith groups abundant and easily visible to the unaided eye, appearing as dark spots on leaf surface; on the lower epidermis 1 to 20 cystoliths per mm.^{2} Druses occurring in cells of phloem, mesophyll, bundle sheath, and bundle extension; styloids present in living cells of all tissues.

Trema (5). Multicellular trichomes comprising a linear row of cells on both leaf surfaces of all species except in *Trema amboinensis* and *T. canescens* occurring only on the lower epidermis. Multicellular stalked trichomes with an enlarged terminal cell on both surfaces of *T. lamarckiana, T. micrantha,* and *T. orientalis*.

Leaves with an entire margin, overall venation pattern "perfect" acrodromous in *T. canescens*, and "imperfect" acrodromous for all other species; terminal tracheary elements in the areole lacking a bundle sheath; mesophyll is divided into 1 to 4 palisade layers; a loose spongy layer present (except compact in *T. amboinensis* and variable in *T. lamarckiana*; bundle sheath extensions present on major veins.

Lower epidermis quite uneven in most species due to prominent ridges and valleys formed by veins (FIGURE 15); *Trema orientalis* with cuticular ridges on both epidermal layers; pegged cystoliths present in enlarged cells and in unicellular hairs of the upper and lower epidermis of *Trema lamarckiana* and *T. micrantha* but only in the upper epidermis of *T. amboinensis*, *T. canescens*, and *T. orientalis*. Cystoliths per mm.^{2} ranging from 27 to 48 for the upper epidermis and from 13 to 16 for the lower; druses found in mesophyll, bundle sheath, bundle sheath extension, and phloem cells; prismatic crystals in phloem and bundle sheath; styloids in living cells of all tissues in *T. micrantha*.

Parasponia (1). Leaf margins serrate and overall venation pattern "simply" craspedodromous; terminal tracheary elements in the areole lacking a bundle sheath; mesophyll divided into a uniseriate layer and a loose spongy layer; bundle sheath extensions poorly developed or lacking.

Pegged cystoliths found in enlarged cells and hairs of both the upper and lower epidermis (10 per mm.^{2} in the upper epidermis and 35 per mm.^{2} in the lower); druses present in the cells of the mesophyll, bundle sheath,

and phloem; mineral placks covering several cells in both upper and lower epidermis.

Aphananthe (*2*). Unicellular hairs barbed; leaf margins serrate, overall venation pattern "simply" craspedodromous in *Aphananthe aspera* and brochidodromous in *A. philippinensis*; terminal tracheary elements in the areole without a sheath; mesophyll with 1 or 2 palisade layers and a loose spongy layer; major veins have bundle sheath extensions.

Pegless cystoliths found in enlarged cells of both upper and lower epidermis; druses in cells of the mesophyll, bundle sheath, and phloem; *Aphananthe philippinensis* with prismatic crystals in the bundle sheath, bundle sheath extension, and phloem; mineral placks in both upper and lower epidermis.

Mirandaceltis (*1, 2*). Some unicellular hairs barbed; leaves with entire margin and overall venation pattern brochidodromous; terminal tracheary elements lacking bundle sheath in the areole; mesophyll divided into 1 or 2 palisade layers and a tight spongy layer; bundle sheath extensions either absent or weakly developed.

Periclinal walls of the upper epidermis, and to a lesser extent of the lower, thickened; pegless cystoliths present in enlarged cells or hairs on upper epidermis; druses present in cells of mesophyll, bundle sheath, and phloem; prismatic crystals found in the two latter tissues; styloids found in the mesophyll.

Gironniera (*5*). *Gironniera parvifolia* and *G. nervosa* with some barbed unicellular hairs; multicellular trichomes on lower epidermis only in *G. nervosa*.

Leaf margins entire and overall venation pattern brochidodromous; terminal trachery elements in the areoles surrounded by round to oval parenchyma cells; mesophyll divided into 1 or 2 palisade layers and a loose spongy layer; major veins with a bundle sheath extension.

Pegless cystoliths in enlarged cells of lower epidermis; druses found in cells of mesophyll, bundle sheath, bundle sheath extension, and phloem; prismatic crystals found in cells of the bundle sheath, bundle sheath extension, and phloem of *G. cuspidata*, *G. nervosa*, and *G. nitida*; styloids in mesophyll and epidermal cells of *G. nervosa*.

Chaetachme (*1*). Leaf margin entire, overall venation pattern brochidodromous; terminal tracheary elements in the areole surrounded by a bundle sheath; mesophyll divided into 1 or 2 palisade layers and a loose spongy layer; bundle sheath extensions occurring only from major veins.

Enlarged cells containing mucilage in upper epidermis; druse and prismatic crystals found in bundle sheaths.

Lozanella (*1*). Leaf margin serrate, overall venation pattern brochido-

dromous; terminal tracheary elements surrounded by a parenchyma sheath in the areole; mesophyll composed of 1 or 2 palisade layers and a loose spongy layer; major veins with bundle sheath extensions.

Cuticular ridges present on both upper and lower epidermis; pegless cystoliths in enlarged cells and in hairs of both upper and lower epidermis; druses in cells of the mesophyll, bundle sheath, and phloem.

Wood

Secondary xylem of Ulmaceae is variable, but the following features are common to all members. Vessel elements ligulate to eligulate; intervascular pitting alternate, pits elongate to circular in outline; fibers with simple to slightly bordered slit-like pits. Unilaterally compound pitting common between both axial and ray parenchyma and vessel elements. Pores angular to circular; vascular rays uniseriate, biseriate, and multiseriate; ray cells thick walled in all species.

Phyllostylon (1). Wood diffuse porous; pore distribution 79 percent solitary, 19 percent radial multiples of 2 to 4 cells, and 2 percent clusters of 3 cells; average pore diameter 53 μ with a range of 35 to 70 μ; vessel element wall thickness from 1.5 to 4 μ; perforations simple; end wall angles from 57 and 90°; inter-vascular pits ranging in diameter from 6 to 7 μ; average length of vessel elements 187 μ with a range of 135 to 240 μ; fiber wall thickness from 4.5 to 5.5 μ; average fiber length 903 μ with a range of 690 to 1215 μ.

All vascular rays homocellular and comprised of procumbent cells; uniseriate rays ranging in height from 3 to 11 cells and from 45 to 200 μ; biseriate and multiseriate rays ranging in height from 7 to 65 cells and from 100 to 900 μ, and ranging in width from 2 to 4 cells and from 15 to 35 μ; prismatic crystals observed in some ray cells.

Axial parenchyma vasicentric and confluent; vessel-ray and vessel-axial parenchyma pitting alternate, pits ranging in diameter from 2.5–5 μ

Holoptelea (2, 3). All woods diffuse porous; pore distribution is 61 to 80 percent solitary, 18 to 35 percent radial multiples of 2 to 4 cells, and 2 to 4 percent clusters of 3 to 11 cells; average pore diameters ranging from 92 to 110 μ, the total range of diameters from 50 to 170 μ; wall thickness of vessel elements ranging from 2.5 to 3.5 μ; perforations simple; end wall angles of vessel elements ranging from 40 to 90°; tyloses in vessel elements of *H. grandis*; average vessel element length ranging from 273 to 284 μ, the total range of lengths from 148 to 370 μ.

Fiber wall thickness from 2 to 3.5 μ; average fiber length from 1169 to 1428 μ with a total range of lengths from 925 to 1702 μ.

Homocellular uniseriate, biseriate, and multiseriate vascular rays comprised of procumbent cells; uniseriate rays few in comparison with the storied biseriate and multiseriate rays. Uniseriate rays ranging in height from 2 to 12 cells and from 60 to 225 μ; biseriate and multiseriate rays

ranging in height from 6 to 57 cells and from 95 to 750 μ; width of rays from 2 to 5 cells and from 10 to 55 μ.

Axial parenchyma vasicentric, aliform, and confluent in all specimens; pitting of vessel-ray and vessel-axial parenchyma alternate, pit diameters ranging from 2.5 to 6 μ.

Planera (1, 3). Two specimens of *Planera aquatica* (USw21789 and Yw6699) diffuse porous; Yw11169 ring porous. Pore distribution 32 to 40 percent solitary, 18 to 35 percent radial multiples of 2 to 4 cells, and 39 to 46 percent clusters of 3 to 9 cells. Average pore diameter 38 μ for the diffuse porous specimens, with a total range of 20 to 55 μ. Average pore diameter of 34 μ for the ring porous specimen and a range from 20 to 55 μ for the early portion of the ring, an average pore diameter of 25 μ and a range from 20 to 35 μ for the last formed portion of the ring. Vessel wall thickness from 0.5 to 3 μ; perforations simple in all three specimens; however, vestigial bars also occurring in the ring porous specimen. End wall angles of vessel elements varying from 24 to 90°; intervascular pit diameters from 5 to 7 μ; average vessel element length from 180 to 450 μ; all vessel elements usually with spiral thickenings.

Imperforate tracheary elements comprised of fiber-tracheids with slightly to prominently bordered pits and vascular tracheids; many vascular tracheids have spiral thickenings. Average lengths of fiber-tracheids from 817 to 885 μ; total range of lengths from 375 to 1485 μ. Some storying of fiber-tracheids occurs in Yw11169.

Vascular rays homocellular; uniseriate rays ranging in height from 2 to 19 cells and from 50 to 400 μ; biseriate and multiseriate rays ranging in height from 5 to 63 cells and from 85 to 1135 μ are from 2 to 6 cells and from 15 to 75 μ in width; prismatic crystals observed in some ray cells, which are sometimes enlarged.

Axial parenchyma diffuse, banded, terminal, and vasicentric; crystals and dark staining contents observed in some axial parenchyma cells; vessel-ray pitting and vessel-axial parenchyma pitting alternate, pits ranging in diameter from 2 to 3 μ.

Ulmus (33, 55). Wood specimens examined ring porous; pores often oriented in wavy tangential lines (FIGURE 16); pore clusters and solitary pores most numerous and radial multiples the least prevalent type of pore distribution; decrease in percentage of clusters usually correlated with a corresponding increase in percentage of solitary pores, little or no change occurring in the percentage of radial multiples; solitary pore distribution from 14 percent in *Ulmus wallichii* to 63 percent in *U. pumila* var. *arborea*; clusters from 32 percent in the latter species to 81 percent in *U. montana*. In *U. canescens*, *U. carpinifolia*, *U. laevis*, *U. macrocarpa*, *U. parvifolia*, *U. pumila*, *U. rubra*, *U. sieboldii*, and *U. uyematsii* no radial multiples occur; in *U. americana* radial multiples accounted for 16 percent of the pore distribution. Number of cells per radial multiple from 2 to 4 and the number per cluster from 3 to 28.

Average pore diameter ranges from 53 μ in *U. pumila*, to 211 μ in *U. glabra* in the first formed portion of the ring, and from 19 μ in *U. rubra* to 53 μ in *U. major* in the last formed portion; vessel wall thickness ranges from 1.5 to 8 μ.

Mostly simple perforations in all species; *Ulmus laevis*, *U. major*, *U. rubra*, *U. serotina*, and *U. stricta* having scalariform perforation plates with one bar (FIGURE 17); *Ulmus alata*, *U. americana*, *U. crassifolia*, *U. glabra*, *U. hollandica* var. *major*, *U. laevis*, *U. macrocarpa*, *U. major*, *U. procera*, *U. pumila*, *U. rubra*, *U. scabra*, *U. serotina*, *U. stricta*, *U. thomasii*, and *U. wallichii* having vestigial bars on perforation plates. Only vessel elements of small diameters with vestigial bars or scalariform perforations (FIGURE 18); vessel element end wall angles from 18 to 90°; most species with at least some vessels with 90° end walls; in general, the greater the diameter of the vessel element, the closer the end wall angle to 90°.

Ulmus alata, *U. carpinifolia* var. *suberosa*, *U. glabra*, *U. laciniata*, *U. macrocarpa*, *U. nitens*, *U. rubra*, *U. scabra*, and *U. stricta* all with some opposite intervascular pitting; diameters of the intervascular pits from 5.5 to 10 μ.

Average vessel element lengths range from 170 μ in *U. thomasii* to 381 μ in *U. major*; the range of all vessel element lengths varying from 111 to 481 μ; tyloses found only in *U. crassifolia* and *U. scabra*.

Imperforate tracheary elements include vascular tracheids and fibers; wall thickness of fibers ranges from 1.5 to 5.5 μ; average lengths of fibers range from 779 μ in *U. carpinifolia* to 1782 μ in *U. montana*; total range of lengths for all specimens is 660 to 2146 μ.

Vascular rays of all species homocellular, comprised of procumbent cells; unicellular rays ranging in height from 2 to 21 cells and from 20 to 230 μ. Biseriate and multiseriate rays ranging in height from 3 to 76 cells and from 50 to 1375 μ; these rays ranging in width from 2 to 19 cells and from 10 to 200 μ; vessel-ray pitting mostly alternate; however, species with some opposite pitting are: *U. alata*, *U. carpinifolia* var. *suberosa*, *U. glabra*, *U. hollandica* var. *major*, *U. macrocarpa*, *U. major*, *U. nitens*, *U. rubra*, *U. scabra*, and *U. stricta*. Diameter of vessel-ray pits ranges from 2.5 to 5 μ.

Axial wood parenchyma mostly vasicentric with some aliform in *U. crassifolia* and some confluent in *U. alata*, *U. americana*, *U. scabra*, and *U. thomasii*, most species showing terminal axial parenchyma. Vessel-axial parenchyma pitting mostly alternate with some opposite in *U. alata*, *U. carpinifolia* var. *suberosa*, *U. glabra*, *U. laciniata*, *U. macrocarpa*, *U. major*, *U. nitens*, *U. plotii*, *U. rubra*, *U. scabra*, *U. serotina*, *U. stricta*, *U. suberosa*, and *U. thomasii*.

Storying of vessel elements and some fibers occurs in *U. alata*, *U. glabra*, *U. scabra*, and *U. serotina*. Prismatic crystals present in ray cells of *U. americana*, *U. major*, *U. montana*, *U. plotii*, *U. rubra*, *U. scabra*, *U. sieboldii*, *U. thomasii*, and *U. uyematsii*; prismatic crystals in enlarged axial parenchyma cells of *U. laciniata*, *U. major*, and *U. scabra*. Strands of

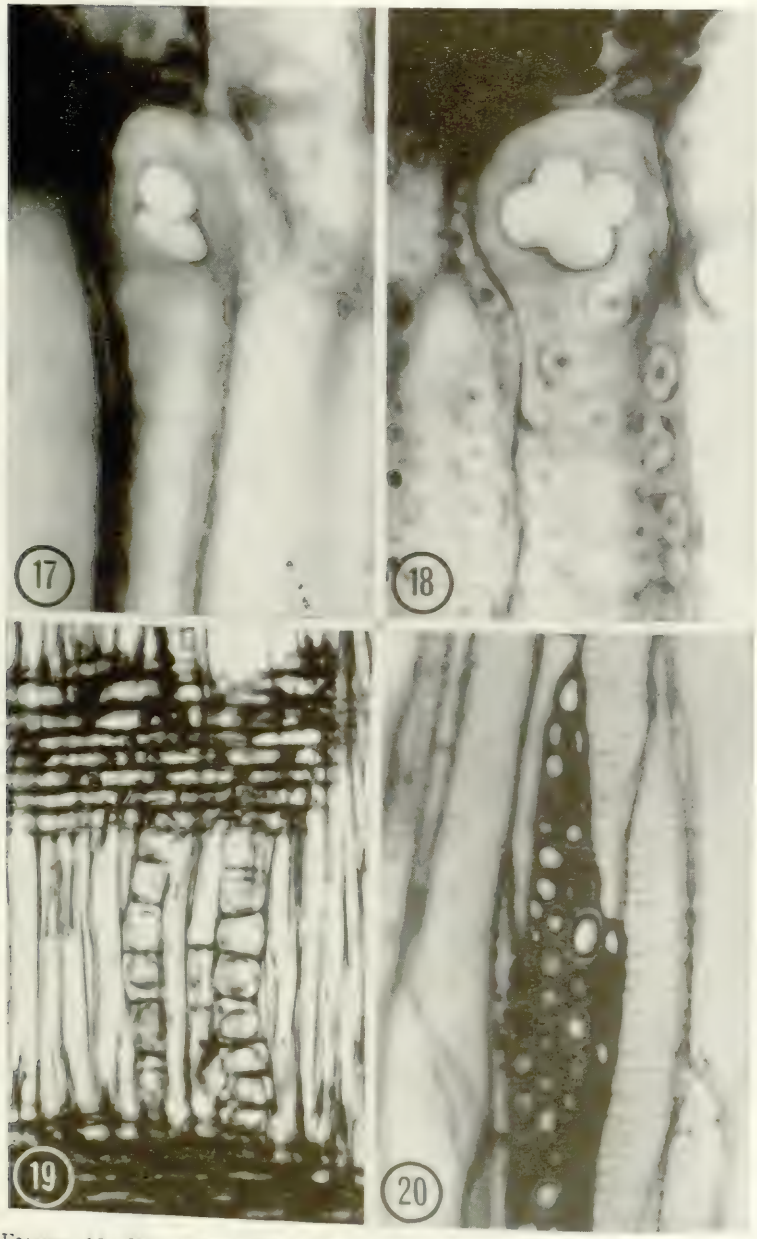

FIGURE 17. *Ulmus serotina*. Radial wood section illustrating a scalariform perforation plate with one bar. × 730. 18. *Ulmus serotina*. Radial wood section showing a perforation plate with vestigial bars. × 730. 19, *Ulmus major*. Radial wood section with crystal strands, × 200. 20, *Ulmus rubra*. Tangential wood section with spiral thickenings on the walls of the vessel elements. × 330.

parenchyma containing prismatic crystals (FIGURE 19) in all species except *U. laciniata*, *U. montana*, *U. procera*, *U. scabra*, and *U. stricta*. Dark staining deposits in many vascular ray cells and axial wood parenchyma cells.

Spiral thickenings on the walls of small vessels and vascular tracheids of all species (FIGURE 20).

Chaetoptelea (1, 2). The names *Chaetoptelea mexicana* Liebm. and *Ulmus mexicana* (Liebm.) Planch. are synonymous; some botanists recognizing *Chaetoptelea* as a distinct genus and others not. For this reason, specimens bearing both binomials are treated in the same section here under *Chaetoptelea*.

Wood ring porous; pore distribution 80 percent solitary, 12 percent radial multiples of 2 to 4 cells, and 8 percent clusters of 3 or 4 cells. Average pore diameters for the first formed portion of the growth ring 150 μ with a range of 25 to 215 μ. Average pore diameters for the last formed portion of growth ring 90 μ, with a range of 40 to 200 μ; vessel wall thickness from 1 to 7 μ; perforations simple; end wall angles range from 44 to 90°; intervascular pit diameters from 3.5 to 6.5 μ. Average vessel element length is 300 μ with a total range of 148 to 407 μ; tyloses found in *C. mexicana*.

Imperforate tracheary elements include vascular tracheids and fibers. Fiber wall thickness from 1 to 3 μ; average fiber length is 1660 μ with a total range of 1221 to 2072 μ.

Vascular rays homocellular, comprised of procumbent cells. Uniseriate rays ranging in height from 2 to 7 cells and 25 to 120 μ. Biseriate and multiseriate rays ranging in height from 4 to 48 cells and 60 to 725 μ, in width from 2 to 8 cells and 15 to 75 μ. Dark staining materials found in some ray cells.

Axial parenchyma vasicentric, aliform, confluent, and terminal; vessel-ray and vessel-axial parenchyma pitting alternate; pits ranging in diameter from 3.5 to 6.5 μ; prismatic crystals and dark staining deposits in some ray cells; crystalliferous strands present.

Celtis (40, 50). Wood ring porous in *Celtis australis*, *C. bungeana*, *C. jessoensis*, *C. koraiensis*, *C. laevigata*, *C. lindheimeri*, *C. occidentalis*, *C. pumila*, *C. reticulata*, *C. sinensis*, *C. tenuifolia*, *C. tournefortii*, and *C. yunnanensis*, diffuse porous in *C. adolphi-friderici*, *C. asperifolia*, *C. cinnamomea*, *C. crenato-serrata*, *C. harperi*, *C. iguanaea*, *C. kraussiana*, *C. latifolia*, *C. luzonica*, *C. pacifica*, *C. pallida*, *C. paniculata*, *C. philippinensis*, *C. rigescens*, *C. riticnsis*, *C. schippii*, *C. soyauxii*, *C. swartzii*, *C. tala*, *C. trinervia*, *C. ugandensis*, *C. wightii*, and *C. zenkeri*. The genus may be divided into two groups based upon pore distribution and porosity: ring porous species having 42 to 85 percent solitary pores, 14 to 52 percent clusters of 3 to 30 cells, and 0 to 12 percent radial multiples of 2 to 4 cells (FIGURE 21). Diffuse porous species have 59 to 90 percent solitary

pores, 9 to 49 percent radial multiples of 2 to 10 cells, and 0 to 6 percent clusters of 3 to 8 cells (FIGURE 22).

Pore diameters for the early part of the growth ring in ring porous species range from 58 to 191 μ with a total range of 20 to 265 μ; for the last formed portion of the ring diameters range from 20 to 40 μ with a total range of 15 to 100 μ. Average pore diameters for diffuse porous species range from 49 to 169 μ with a total range of 15 to 225 μ; vessel element wall thickness ranges from 1.5 to 6 μ; all diffuse porous species having only simple perforations; all ring porous species, except *Celtis lindheimeri* with exclusively simple perforations, having at least some perforations with vestigial bars in addition to simple perforations; *Celtis jessoensis*, *C. laevigata*, and *C. pumila* also having scalariform plates with one bar in addition to the vestigial bars; end wall angles varying from 10 to 90°; all species having at least some vessels with 90° end walls.

Celtis bungeana and *C. reticulata* with some opposite intervascular pitting; pitting crowded in *C. iguanaea*, *C. kraussiana*, *C. pacifica*, *C. philippinensis*, and *C. wightii*; intervascular pit diameters ranging from 2 to 9 μ; average vessel element lengths ranging from 170 to 455 μ; total range of lengths 111 to 666 μ; tyloses found in *C. iguanaea*, *C. laevigata*, *C. lindheimeri*, *C. reticulata*, and *C. ritiensis*.

Vascular tracheids present in ring porous species, absent in diffuse porous species; fiber wall thickness ranging from 1 to 5.5 μ; average fiber length range is 717 to 1709 μ with a total range of 518 to 2220 μ.

It is difficult to determine whether the uniseriate rays are homocellular, heterocellular, or both; in tangential section some of the component cells appear upright, but in radial section all cells are procumbent, radial dimensions exceeding the axial dimensions. There is a problem in correlating the appearance of a ray in radial section with its appearance in tangential section; however, if these so-called "upright" cells in tangential view were truly upright, they would not have been so scarce in radial section. Therefore, the uniseriate rays will be designated homocellular, even though some may be technically heterocellular. Whenever a similar condition is encountered in other genera, for the sake of uniformity in this paper such a uniseriate ray type is referred to as the Celtis type. Some multiseriate rays classed as heterocellular are conceivably homocellular, but a detailed statistical analysis of the cellular composition of rays from tangential and radial sections is beyond the scope of this paper.

Biseriate and multiseriate rays heterocellular with procumbent cells in the body of the ray and upright cells on the margins; height of unicellular rays from 2 to 25 cells and 20 to 1000 μ for all species; height of biseriate and multiseriate rays ranging from 3 to 115 cells and 40 to 1800 μ, width ranging from 2 to 14 cells and 10 to 195 μ. Two species, *Celtis kraussiana* and *C. laevigata*, showed a tendency towards formation of sheath ray cells since some of the marginal cells are elongated.

Vessel-ray parenchyma pitting and vessel-axial parenchyma pitting are considered together since they are similar in arrangement and size. All species investigated show what can be called alternate pit arrangement,

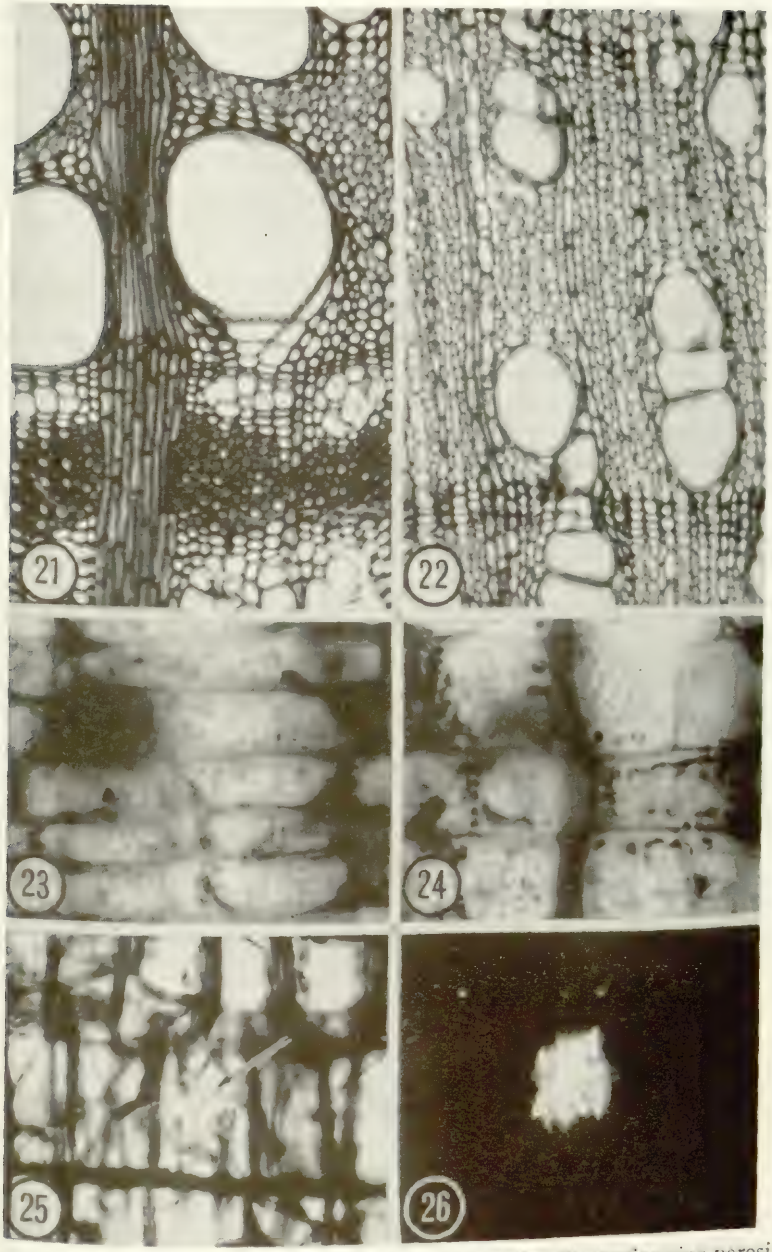

FIGURE 21, *Celtis reticulata*. Transverse wood section illustrating ring porosity, × 120. 22. *Celtis pallida*. Transverse wood section illustrating diffuse porosity, × 220. 23 and 24. *Celtis pacifica*. Radial wood sections illustrating variable vessel-ray pitting. × 660. 25. *Lozanella enantiophylla*. Radial wood section with a druse crystal in a ray cell, × 330; 26. *the same*. The same druse crystal as in FIGURE 25, under polarized light. × 330.

the pits having a circular to elongate outline; some species also had pit arrangements and shapes not easily described; FIGURES 23 and 24, used to illustrate these different patterns, for which the term "variable" will be used here and wherever such arrangements occur in other genera.

Celtis cinnamomea, *C. laevigata* var. *smallii*, and *C. lindheimeri* with some opposite arrangement in addition to alternate; *Celtis pacifica* and *C. ritiensis* with mostly transitional to opposite arrangements; total range in pit diameters for vessel-ray parenchyma pitting and vessel-axial parenchyma pitting is 1.5 to 7 μ.

Axial parenchyma is vasicentric, aliform, and confluent; most species also with terminal parenchyma; *Celtis pumila* with diffuse in addition to vasicentric parenchyma; *Celtis iguanaea*, *C. occidentalis*, *C. pacifica*, *C. paniculata*, *C. paniculata* var. *multiseriata*, *C. pumila*, *C. swartzii*, *C. trinervia*, and *C. ugandensis* with banded parenchyma in addition to the paratracheal types.

Spiral thickenings occur on small vessel elements of all ring porous species; prismatic crystals found in ray and axial parenchyma of all species except *C. adolphi-friderici* and *C. ugandensis*.

Pteroceltis (1, 2). Wood diffuse porous; pore distribution 75 percent solitary, 24 percent radial multiples of 2 to 5 cells and 1 percent clusters of 3 to 4 cells; average pore diameter is 55 μ with a total range of 27 to 90 μ; vessel element wall thickness ranging from 2.5 to 5 μ; perforations simple; end wall angles ranging from 19 to 90°; intervascular pitting crowded, range of pit diameters from 1.5 to 3 μ; average vessel element length 250 μ with a total range of 75 to 390 μ; fiber wall thickness ranging from 2 to 4.5 μ; average fiber length 870 μ with a total range of 510 to 1260 μ.

Uniseriate vascular rays homocellular (Celtis type), biseriate and multiseriate rays heterocellular; height of unicellular rays 2 to 12 cells and 85 to 390 μ; biseriate and multiseriate rays ranging in height from 4 to 41 cells and 75 to 760 μ; width varying from 2 to 5 cells and 10 to 45 μ; dark staining deposits and prismatic crystals in some ray cells; cells containing crystals usually enlarged.

Axial parenchyma vasicentric and confluent; vessel-ray and vessel-axial parenchyma alternate, pits ranging in diameter from 1.5 to 3 μ; prismatic crystals in some axial parenchyma cells.

Ampelocera (4, 5). Wood diffuse porous; pore distribution is 74 to 90 percent solitary, 9 to 22 percent radial multiples of 2 to 5 cells, and 0 to 5 percent clusters of 3 to 4 cells; average pore diameters ranging from 73 to 124 μ with a total range of 30 to 170 μ; vessel wall thickness 3 to 5.5 μ; perforations simple; end wall angles ranging from 30 to 90°; intervascular pit diameters from 6 to 10.5 μ; average vessel element length ranging from 222 to 277 μ with a total range from 148 to 370 μ.

Some fibers septate; fiber wall thickness ranging from 3 to 4.5 μ;

average fiber length ranging from 1088 to 1310 μ with a total range from 888 to 1554 μ.

Uniseriate, biseriate, and multiseriate rays are homocellular, comprised of procumbent cells; uniseriate rays not abundant, ranging in height from 2 to 13 cells and 50 to 225 μ; biseriate and multiseriate rays ranging in height from 5 to 50 cells and 80 to 810 μ; width ranging from 2 to 5 cells and 10 to 40 μ; prismatic crystals occurring in some ray cells.

Axial parenchyma banded in *A. cubensis*, diffuse in *A. edentula*, and terminal in *A. edentula* and *A. glabra*; all species have vasicentric, aliform, and confluent parenchyma; vessel-ray and vessel-axial parenchyma pitting is alternate, the pit diameters ranging from 2.5 to 5 μ.

Zelkova (3, 4). Wood ring porous; pore distribution is 26 to 38 percent solitary, 53 to 73 percent clusters of 3 to 25 cells, and 0 to 8 percent radial multiples of 2 to 3 cells; average pore diameters in the first formed portion of the growth ring ranging from 73 to 150 μ with a total range from 15 to 55 μ; average pore diameter for the last formed part of the growth ring ranging from 23 to 41 μ with a total range of 15 to 55 μ; vessel wall thickness ranging from 1.5 to 5 μ; perforations scalariform (1 bar), simple with vestigial bars, and simple; end wall angles varying from 15 to 90°; intervascular pit diameters ranging from 5 to 9 μ; average vessel element length from 185 to 207 μ with a total range from 111 to 259 μ; tyloses found in *Zelkova serrata* and *Z. sinica*; spiral thickenings found in small vessel elements; storying of vessels in *Z. keakii* and *Z. serrata*.

Imperforate tracheary elements include vascular tracheids and fibers with bordered pits. Some fiber-tracheids are septate in *Z. keakii* and *Z. serrata*; fiber-tracheid wall thickness varying from 2 to 3.5 μ. Average fiber-tracheid length ranges from 1024 to 1687 μ with a total range from 888 to 1998 μ.

Uniseriate rays homocellular (Celtis type), not abundant; biseriate and multiseriate rays mostly homocellular with procumbent cells in *Z. keakii* and *Z. serrata*; but both homocellular and heterocellular in *Z. sinica*; homocellular uniseriate rays ranging in height from 2 to 11 cells and 60 to 260 μ; biseriate and multiseriate rays ranging in height from 6 to 90 cells and 110 to 1165 μ, in width from 2 to 10 cells and 10 to 115 μ; prismatic crystals and dark contents found in some ray cells; some crystal containing cells enlarged.

Axial parenchyma vasicentric; vessel-ray and vessel-axial parenchyma pitting alternate with pit diameters from 2.5 to 5 μ; prismatic crystals and dark deposits occurring in some cells; crystalliferous strands found in *Z. keakii*.

Hemiptelea (1, 2). Wood ring porous; pore distribution 42 percent solitary, 50 percent clusters of 3 to 15 cells, and 8 percent radial multiples of 2 to 5 cells; average pore diameter for the early part of the growth ring 70 μ with a range from 15 to 165 μ; average for the last formed portion of the ring is 22 μ with a range from 10 to 30 μ; perforations scalariform

(1–2 bars), simple with vestigial bars, and simple; end wall angles varying from 14 to 90°; intervascular pits ranging in diameter from 3.5 to 6.5 μ; average vessel element length 220 μ with a range of 143 to 296 μ; small vessel elements with spiral thickenings; some storying of vessels occurring.

Imperforate tracheary elements include vascular tracheids and fibers; some fibers septate; vascular tracheids with spirals; fiber wall thickness ranging from 2 to 5 μ; average fiber length 1100 μ with a range from 888 to 1332 μ.

Uniseriate rays homocellular (Celtis type) with procumbent cells; ranging in height from 3 to 12 cells and 70 to 300 μ; biseriate and multiseriate rays heterocellular; height ranging from 6 to 45 cells and 95 to 675 μ, width ranging from 2 to 28 cells and 25 to 280 μ; prismatic crystals and dark staining materials found in some ray cells.

Axial parenchyma vasicentric and terminal; vessel-ray and vessel-axial parenchyma pitting alternate with pit diameters from 1.5 to 2.5 μ.

Trema (9, 11). Wood diffuse porous; pore distribution 53 to 88 percent solitary, 6 to 42 percent radial multiples of 2 to 4 cells, and 0 to 6 percent clusters of 3 to 6 cells; pore diameter averaging from 80 to 117 μ with a total range of 15 to 165 μ; perforations simple; end wall angles varying from 10 to 90°; intervascular pitting crowded in *Trema guineënse*, *T. micrantha*, and *T. vieillardii*; pit diameters ranging from 2.5 to 6.5 μ; average vessel element lengths ranging from 281 to 566 μ with a total range from 185 to 832 μ; vessels in *T. guineënse*, *T. lamarckiana*, and *T. micrantha* with tyloses; *Trema bracteolata* with septate fibers; fiber wall thickness ranging from 1 to 5 μ; average fiber lengths ranging from 777 to 1295 μ with a total range from 518 to 1702 μ.

Uniseriate rays homocellular (Celtis type), ranging in height from 2 to 21 cells and 55 to 785 μ; biseriate and multiseriate rays heterocellular, ranging in height from 4 to 7 cells and 100 to 1875 μ and in width from 2 to 7 cells and 10 to 60 μ; dark staining material occurring in many ray cells; prismatic crystals found in ray cells of *Trema vieillardii*.

Axial parenchyma vasicentric; vessel-ray and vessel-axial parenchyma pitting "variable" to alternate; pit diameters ranging from 2.5 to 6.5 μ.

Parasponia (1). Wood diffuse porous; pore distribution 77 percent solitary, 20 percent radial multiples of 2 to 3 cells, and 3 percent clusters of 3 cells; average pore diameter 143 μ with a range from 95 to 225 μ; vessel element walls ranging in thickness from 2 to 3.5 μ; perforations simple; end wall angles varying from 16 to 90°; intervascular pitting crowded with a range of pit diameters 6 to 9 μ; average vessel element length is 381 μ with a range from 240 to 450 μ; fiber thickness varying from 2 to 3 μ; average fiber length 890 μ with a range from 456 to 1110 μ.

Uniseriate rays homocellular, comprised of procumbent cells and ranging in height from 2 to 13 cells and 75 to 390 μ; biseriate and multiseriate

rays heterocellular, ranging in height from 5 to 38 cells and 160 to 860 μ, in width from 2 to 4 cells and 20 to 75 μ; dark staining deposits and prismatic crystals found in some ray cells.

Axial parenchyma vasicentric and terminal; dark staining deposits and prismatic crystals found in some cells; vessel-ray and vessel-axial parenchyma pitting alternate with a pit diameter range from 5 to 7.5 μ.

Aphananthe (2). Wood diffuse porous; pore distribution 66 percent solitary, 30 percent radial multiples of 2 to 4 cells, and 4 percent clusters of 3 to 5 cells; average pore diameter 85 μ with a total range of 50 to 150 μ; vessel wall thickness ranging from 2.5 to 5.5 μ; perforations simple; end wall angles of vessel elements ranging from 15 to 90°; intervascular pit diameters ranging from 3.5 to 6.5 μ; average vessel element length 290 μ with a total range from 222 to 518 μ; tyloses found in vessels of *A. philippinensis*; fiber wall thickness ranging from 2.5 to 4.5 μ; average fiber length 1190 μ with a total range from 1036 to 1443 μ.

Uniseriate rays homocellular (Celtis type) comprised of procumbent cells ranging in height from 3 to 10 cells and 65 to 235 μ; biseriate and multiseriate rays heterocellular, ranging in height from 3 to 43 cells and 65 to 525 μ, in width 2 to 5 cells and 10 to 40 μ; dark staining deposits found in some ray cells.

Axial parenchyma is vasicentric, confluent, and terminal; *Aphananthe philippinensis* also exhibits some banding; vessel-ray and vessel-axial parenchyma pitting alternate to "variable," pit diameters ranging from 2.5 to 6.5 μ.

Mirandaceltis (1). Wood diffuse porous; pore distribution 73 percent solitary, 20 percent radial multiples of 2 to 3 cells, and 7 percent clusters of 3 to 6 cells; average pore diameter 57 μ with a range from 35 to 85 μ; vessel wall thickness 2.5 to 5 μ; perforations simple; end wall angles ranging from 35 to 90°; intervascular pitting crowded with a pit diameter from 3 to 4 μ; average vessel element length 307 μ, ranging from 148 to 407 μ; tyloses present in vessels.

Fiber wall thickness 2 to 3 μ; average fiber length 828 μ with a range from 740 to 962 μ.

Uniseriate rays homocellular (Celtis type), ranging in height from 2 to 15 cells and 65 to 275 μ; biseriate and multiseriate rays heterocellular, ranging in height from 6 to 30 cells and 100 to 510 μ, in width from 2 to 4 cells and 25 to 40 μ; some ray cells with prismatic crystals and dark staining deposits.

Axial parenchyma is vasicentric, confluent, and terminal; prismatic crystals and dark staining contents found in some cells; vessel-ray and vessel-axial parenchyma pitting alternate to "variable"; pits ranging in diameter from 2.5 to 5 μ.

Gironniera (5, 9). Wood diffuse porous; pore distribution from 51 to 92 percent solitary, 6 to 46 percent radial multiples of 2 to 7 cells, and

0 to 6 percent clusters of 3 to 8 cells; pore diameters ranging from 88 to 186 μ with a total range from 40 to 255 μ; vessel wall thickness ranging from 2.5 to 5 μ; perforations simple; end wall angles varying from 30 to 90°; intervascular pit diameters ranging from 2.5 to 12.5 μ; average vessel element lengths ranging from 333 to 407 μ with a total range of 148 to 1147 μ; tyloses present in *Gironniera celtidifolia*.

Some fibers septate in *Gironniera celtidifolia*; fiber wall thickness varying from 1.5 to 6.5 μ; average fiber length ranging from 1188 to 1795 μ with a total range from 814 to 2590 μ.

Uniseriate rays homocellular (Celtis type); uniseriate rays of *Gironniera cuspidata* and *G. nitida* ranging in height from 2 to 13 cells and 60 to 275 μ; biseriate and multiseriate rays ranging in height from 5 to 62 cells and 85 to 1115 μ and in width from 2 to 5 cells and 15 to 45 μ; uniseriate rays of *G. celtidifolia*, *G. nervosa*, and *G. subaequalis* ranging in height from 2 to 18 cells and 90 to 1335 μ; biseriate and multiseriate rays ranging in height from 5 to 89 cells and 230 to 2475 μ, in width from 2 to 14 cells and 20 to 205 μ; prismatic crystals present in ray cells of *G. cuspidata* and *G. nitida*.

Axial parenchyma vasicentric in *G. nervosa*; vasicentric, confluent, and banded in *Gironniera celtidifolia*, *G. cuspidata*, and *G. nitida*; vasicentric, aliform, and confluent in *G. subaequalis*; prismatic crystals present in some cells of *G. cuspidata* and *G. nitida*; dark deposits present in some ray and axial parenchyma cells; vessel-ray and vessel-axial parenchyma pitting are "variable" to alternate; pit diameters ranging from 2.5 to 10 μ.

Chaetachme (2). Wood diffuse porous; pore distribution 60 percent solitary, 34 percent radial multiples of 2 to 8 cells, and 6 percent clusters of 3 to 7 cells; average pore diameter 78 μ with a range of 35 to 135 μ; vessel wall thickness from 1.5 to 6.5 μ; perforations simple; vessel end wall angles varying from 15 to 90°; intervascular pit diameters from 3.5 to 6.5 μ; average vessel element length 450 μ with a range of 296 to 666 μ; tyloses present in *C. aristata*.

Fibers septate; wall thickness from 1.5 to 5.5 μ; average fiber length 1540 μ with a total range from 1184 to 2146 μ; uniseriate rays homocellular (Celtis type), ranging in height from 2 to 10 cells and 50 to 235 μ; biseriate and multiseriate rays heterocellular, ranging in height from 7 to 96 cells and 65 to 1920 μ, in width from 2 to 5 cells and 20 to 35 μ; dark staining deposits in ray cells of *C. microcarpa*.

Axial parenchyma vasicentric, confluent, and banded; vessel-ray and vessel-axial parenchyma pitting "variable" to alternate; pit diameters from 2.5 to 6.5 μ.

Lozanella (1). Wood diffuse porous; pore distribution 72 percent solitary, 28 percent radial multiples of 2 to 4 cells; average pore diameter 140 μ, ranging from 60 to 200 μ; vessel wall thickness 2 to 3 μ; perforations simple; end wall angles from 36 to 90°; intervascular pit diameters

from 7 to 9 μ; average vessel length 468 μ, ranging from 300 to 630 μ; tyloses present.

Some fibers septate; wall thickness from 3.5 to 5 μ; average fiber length 930 μ with a range from 630 to 1350 μ.

Uniseriate rays homocellular (Celtis type) comprised of procumbent cells, range in height from 2 to 10 cells and 125 to 510 μ; biseriate and multiseriate rays heterocellular, ranging in height from 7 to 91 cells and 200 to 2500 μ, in width from 2 to 7 cells and 40 to 85 μ; druses and dark staining contents present in some ray cells (FIGURES 25, 26).

Axial parenchyma vasicentric, confluent, and banded; some cells with druses; vessel-ray and vessel-axial parenchyma pitting "variable" to alternate; pit diameters from 3.5 to 6.5 μ.

DISCUSSION

The validity of using secondary xylem characters for systematic purposes has been established through the studies of Bailey and Tupper (1918), Frost (1930a, 1930b, 1931), Chalk and Chattaway (1935), Kribs (1935, 1937), Barghoorn (1940, 1941a, 1941b), and many others. Following these basic investigations, application of concepts has provided valuable information on the relationships of many disputed taxa, e.g., Tippo (1938), Heimsch (1942), Stern (1952), and Carlquist (1960). The techniques of systematic wood anatomy and its application to problems in plant phylogeny was summarized by Tippo (1946). Bailey, in 1957, wrote: "The chief trends of evolutionary specialization in the cambium and xylem of dicotyledons are now so reliably established (except in the case of certain patterns of wood parenchyma distribution) that they can be utilized to advantage in studying salient problems of phylogeny and classification." Use of leaf anatomical characters for systematic problems was summarized by Carlquist (1961), who noted, "The leaf is perhaps anatomically the most varied organ of angiosperms, and its anatomical variations often occur closely with generic and specific — occasionally — familial lines."

In any comparative systematic study using only anatomical features would invite misconceptions. Anatomical characters are most useful when employed in conjunction with data from other fields of botanical endeavor. Important correlative data might come from fields of phytochemistry, cytotaxonomy, paleobotany, embryology, morphogenesis, phytogeography, etc. It is important to consider and evaluate studies from these investigative fields and to apply pertinent findings to those from plant anatomy. Consequently, a complex of characters must be examined in an attempt to avoid mistaking convergent evolution for valid genotypic similarities which have resulted from derivation of taxa from common ancestry.

ANATOMY

The anatomical observations made in this study are in basic agreement with previous works. Scalariform perforations are reported here

for the first time in the secondary xylem of some species of *Celtis*, *Hemiptelea*, *Planera*, *Ulmus*, and *Zelkova*.

The Ulmaceae as a family are diverse anatomically. However, there are many anatomical characters of leaf and wood which pervade the entire group. Among the common features in leaves are the anomocytic stomatal apparatus, bulbous-based unicellular trichomes, similar multicellular hairs, parenchymatous bundle sheaths and extensions, presence of silica, calcium carbonate, and mucilage, and all venation patterns basically pinnate. Common features of the xylem include relatively short vessel elements (less than 350 μ long); alternate intervascular pitting; mostly simple perforations; relatively short fibers (less than 900 μ long); simple to slightly bordered fiber pits; uniseriate, biseriate, and multiseriate vascular rays; and some homocellular vascular rays in all genera.

The two tribes can be separated to a greater or lesser extent on the following anatomical grounds:

ULMEAE	CELTEAE
LEAF	
"Simply" craspedodromous venation pattern	Brochidodromous venation pattern
Pegged cystoliths absent	Pegged cystoliths present
WOOD	
Rays homocellular only	Rays homocellular and heterocellular
Vessel-ray and vessel-axial parenchyma pitting alternate	Vessel-ray and vessel-axial parenchyma pitting "variable" to alternate

The ulmaceous genera are more or less distinct anatomically. *Celtis* can be divided into two groups on the basis of ring *versus* diffuse porosity. The ring porous species are similar to *Ulmus* (which is all ring porous) in pore distribution, presence of spirals in small vessel elements, and types of perforation plates (scalariform, simple with vestigial bars, and simple). However, *Celtis* is easily distinguishable by the presence of heterocellular biseriate and multiseriate rays in the secondary xylem, by the brochidodromous venation pattern in the leaf, by the presence of pegged cystoliths and of the compact spongy mesophyll. *Ulmus* is distinguishable from ring porous species of *Celtis* (and from the diffuse porous species as well) in wood anatomy by homocellular biseriate and multiseriate rays and crystalliferous strands, and in leaf anatomy by the "simply" craspedodromous venation pattern in the leaf, loose spongy mesophyll, and lack of pegged cystoliths.

On the basis of floral morphology and geographical distribution *Celtis* was divided into the subgenera CELTIS, SPONIOCELTIS, SOLENOSTIGMA, and MOMISIA and *Ulmus* into the subgenera OREOPTELEA, DRYOPTELEA, and MICROPTELEA by Planchon (1873). On the basis of external morphology, Rehder (1940) divided *Ulmus* into the sections BLEPHAROCARPUS, CHAETOPTELEA, ULMUS (§ *Madocarpus*), MICROPTELEA, and TRICHOPTELEA. Anatomical evidence neither sustains nor rejects any of these groupings.

In the other Ulmeae, *Phyllostylon* and *Holoptelea* both have cystoliths in the leaves as well as many other leaf characters in common. However, they can be separated on the basis of wood anatomy: *Holoptelea* has only few uniseriate rays, biseriate and multiseriate rays are storied, and ray cells lack crystals; *Phyllostylon* has many uniseriate rays, rays are not storied, and prismatic crystals occur in ray cells. *Planera* is distinguished from *Holoptelea* and *Phyllostylon* by the "simply" craspedodromous venation pattern in the leaf, whereas, *Holoptelea* and *Phyllostylon* show a brochidodromous pattern. In wood anatomy *Planera* is distinguished from *Holoptelea* and *Phyllostylon* by the pore distribution: *Planera* has mostly solitary pores and clusters, *Holoptelea* and *Phyllostylon* have mostly solitary pores and radial multiples. *Planera* has many xylem anatomical features in common with *Ulmus*. However, *Planera* has spiral thickenings in all vessel elements and *Ulmus* only has spirals in small vessel elements.

An apparent anomaly occurs among the studied specimens of *Planera aquatica*, two of these are diffuse porous and the third is ring porous. However, all *Planera* specimens have the characteristic pore distribution of ulmaceous ring porous species (solitary pores and clustered pores highest in percent with radial multiples least in percent). It should also be noted that in the ring porous specimen the difference in pore diameter in the first formed portion of the ring is only nine microns greater than the pore diameters in the last formed portion of the ring. In other ring porous species of the Ulmaceae the first formed pores are two to six times the diameter of the last formed pores. Apparently, *Planera* has the genetic capability of being either diffuse or ring porous. The less pronounced ring porosity in *Planera* is probably the result of the more equable climate of its habitat in the southeastern United States.

Chaetoptelea has many anatomical features in common with *Ulmus*, but the two genera differ in the following points: *Chaetoptelea* has mostly solitary and radial pore multiples, whereas, all *Ulmus* species have mostly solitary and clustered pores; *Chaetoptelea* lacks spiral thickenings in all vessel elements, while all *Ulmus* species have spirals in small vessels. Record and Hess (1943) report spirals in the "smallest vessels of *Chaetoptelea*"; however, none was observed in this study.

In the Celteae, *Celtis* is such a large and diverse genus that anatomically it is difficult to distinguish it from *Pteroceltis*, *Mirandaceltis*, *Gironniera*, and *Chaetachme*. *Ampelocera* is similar to *Celtis* in leaf anatomy, but distinct on the basis of wood anatomy as *Ampelocera* has septate fibers and all homocellular rays while *Celtis* lacks septate fibers and has heterocellular rays. *Zelkova* is distinct because of its "simply" craspedodromous leaf venation pattern, lack of pegged cystoliths, and mostly homocellular rays. *Hemiptelea* is separated from both these genera by the "simply" craspedodromous leaf venation pattern, presence of pegged cystoliths, and storying of vessels. *Trema* has the acrodromous leaf venation pattern, uneven leaf epidermis, and septate fibers in the xylem. *Parasponia* and *Aphananthe* both have a "simply" craspedodromous leaf venation pattern,

but in other anatomical features are quite similar to *Celtis*. *Lozanella* is similar to *Celtis* in all respects except that it has druses in the vascular ray cells. It was not possible in either Celteae or Ulmeae to separate most species within a genus on the basis of wood and leaf anatomy.

PROBLEM GENERA

The question whether *Chaetoptelea* should be a separate genus or part of *Ulmus* cannot be answered on the basis of a few characters. Dr. Leo Hickey of the Smithsonian Institution (personal communication) is able to distinguish fossil *Chaetoptelea* leaves from fossil *Ulmus* leaves on the basis of venation. Standley (1922) stated that "All the species of the latter genus [*Ulmus*], however, have a broadly winged fruit, while in *Chaetoptelea* there is no vestige of a wing, and this probably is a sufficient basis for the maintenance of Liebmann's genus." Leaf anatomy of *Chaetoptelea mexicana* is quite similar to *Ulmus*. In wood anatomy both genera are ring porous, but two distinct differences in the secondary xylem occur: *Chaetoptelea* has mostly solitary and radial pore multiples, whereas, all *Ulmus* species have mostly solitary and clustered pores; *Chaetoptelea* lacks spiral thickenings in vessel elements while all *Ulmus* species have spiral wall thickenings in small vessel elements. Metcalfe and Chalk (1950) state, "The most valuable taxonomic vessel characters are the distribution and pattern of the pores as seen in transverse sections." Thus, it would appear that *Chaetoptelea* as a separate genus may be supported by wood anatomy.

Sharp (1958) created a separate genus, *Mirandaceltis*, for the single species *Celtis monoica* Hemsl. on the following basis: "This genus differs from *Celtis* in the venation of the leaves which resembles that of *Ulmus* . . . The drupaceous fruit is also larger and less spherical than that usually found on *Celtis* . . ." Some differences in leaf anatomy were noted in that some unicellular hairs are barbed in *Mirandaceltis* and not in *Celtis*; cystoliths are of the pegless variety in *Mirandaceltis*, whereas, all *Celtis* species, except *C. schippii*, have pegged cystoliths. It must be stated, however, that the overall venation pattern of *Mirandaceltis* is similar to that in most *Celtis* species (brochidodromous), whereas, in *Ulmus* the venation pattern is "simply" craspedodromous. I find no difficulty in distinguishing the pattern of venation in *Mirandaceltis* from that in *Ulmus*, including the leaf specimens of *Mirandaceltis* illustrated in Sharp (1958). On the basis of wood anatomy *Mirandaceltis* cannot be separated from *Celtis*. The taxonomic status of this genus is questionable and anatomically it seems to be only a minor variant of *Celtis*. However, further study should be undertaken to determine the possible taxonomic importance of the pegged versus unpegged cystoliths.

The genus *Gironniera* contains two subgenera, GIRONNIERA (*Nematostigma* Planch.) [2] with *G. celtidifolia*, *G. nervosa*, and *G. subaequalis* and

[2] According to ICBN, Art. 22, 1966, the name GIRONNIERA must be used for the subgenus containing the type species.

GALUMPITA Blume with *G. cuspidata*, *G. nitida*, and *G. reticulata* (Bentham & Hooker, 1862; Engler & Prantl, 1893). Anatomically the two subgenera are most readily separated by the much larger secondary xylem rays of the former group. Subg. GALUMPITA is reported to have possible affinities with *Chaetachme* (Record, as a footnote to Janssonius, 1932). On the basis of wood and leaf anatomy there are no features which would negate a relationship between subg. GALUMPITA and *Chaetachme*. On the basis of leaf anatomy it is unlikely that subg. GIRONNIERA is related to *Trema*, however, since there are several differences: overall venation pattern is acrodromous in *Trema* and brochidodromous in subg. GIRONNIERA, pegged cystoliths are lacking in subg. GIRONNIERA but present in *Trema*, and the occurrence of a multiple epidermis in *Trema*, absent in *Gironniera* subg. GIRONNIERA. *Trema* and subg. GIRONNIERA are similar in overall wood anatomy.

Subgenus GIRONNIERA is similar to *Parasponia* in wood anatomy, but differs in leaf anatomy, *Parasponia* having neither pegged cystoliths nor barbed hairs, subg. GIRONNIERA having both. Further detailed study of the wood and leaf anatomy is necessary to determine species variation before this problem can be solved.

FAMILY RELATIONSHIPS

The question has been raised whether Ulmaceae should be one family with two subgroups or two separate families. Link (1831) proposed two families, Ulmaceae and Celtaceae (as Celtidaceae). Grudzinskaya (1967) supported this contention and suggested that the Celteae (as Celtideae) has more characters in common with the Moraceae than with the Ulmeae, but not enough to incorporate it into the Moraceae. Grudzinskaya further suggests transferring *Hemiptelea* and *Zelkova* from Celteae to Ulmeae. It should be mentioned that her conclusions were drawn without prior study of the secondary xylem of the Ulmaceae.

The recommendation to split this family in two fails to account for genera with transitional characters in each tribe, e.g., *Ampelocera*, *Phyllostylon*, *Zelkova*, *Planera*, and *Hemiptelea*. Baillon (1880) stated that the "Celtideae, on the one hand, could not be disjoined from the Elms, the fruit of *Planera* being intermediate between the drupes of *Celtis* and the samarae of Ulmus." Lindley (1853) stressed that the Celteae (Celtideae) and Ulmeae should be considered "mere forms of one type." The maintenance of two subgroups within the Ulmaceae has, accordingly, been followed by most taxonomists.

Wood and leaf anatomy shed additional light on this problem by illustrating further transitional characters. *Phyllostylon* has homocellular rays, a character of the Ulmeae, and pegged cystoliths, a character of the Celteae; *Zelkova* has many secondary xylem characters in common with both groups: the venation pattern is like the Ulmeae and the biseriate and multiseriate wood rays are heterocellular (a character of the Celteae) and homocellular (as in Ulmeae). *Hemiptelea* is like *Zelkova* in many

respects and in addition it has pegged cystoliths (as in Celteae). *Ampelocera*, which is placed in, and is like the Celteae in most leaf and wood characteristics, has homocellular biseriate and multiseriate rays (a character of Ulmeae). Even when the secondary rays are considered in other Celteae, the homocellular type is not totally absent since it was noted that homocellular types of transitional nature are found. In the Anatomy portion of the DISCUSSION of this paper is a complete listing of anatomical features held in common by Ulmeae and Celteae.

As far as relating the Ulmaceae to the Moraceae is concerned, most present day systematists acknowledge the naturalness of the Urticales, among them Cronquist (1968), Hutchinson (1969), Taktahjan (1969). A notable exception is Thorne (1963) who thinks that the Urticales in the sense of the taxonomists noted above, particularly of Cronquist, comprise convergent groups. Nair and Sharma (1965), on the basis of pollen studies, state that the Urticales are a homogeneous group. If Urticales is composed of genetically closely related elements, as is conceded by most authorities today, it would not be at all irregular for genera in related families to possess certain common characteristics. That is exactly what occurs between the Moraceae and some members of the Celteae. From the point of view of many morphological and anatomical features, Ulmaceae should be considered a natural taxon with two, more or less distinct subgroups having transitional forms.

When a comparison is made between the relatively small family, Ulmaceae, and the relatively large family, Moraceae (53 genera and 1,400 species), statistical probability of similarities through parallel evolution is very high. The dangers of comparing a small taxon with a large family have been pointed out by Stern and Brizicky (1958).

The separation of the two subgroups within the Ulmaceae into two separate families is not supported by leaf and secondary xylem anatomy. Other features also suggest a cohesiveness within Ulmaceae; the nodal anatomy, for example, is trilacunar throughout the family (Sinnott & Bailey, 1914); the haploid chromosome number of 14 is reported in all genera investigated to date; sieve tube elements are short with slightly oblique to transverse simple sieve plates (Zahur, 1959); and Lebreton (1965), on the basis of flavonoid analysis, supported the distinctness of the Ulmaceae from other families in the Urticales.

GENERAL ANATOMICAL CONSIDERATIONS

The use of the terms loose and compact in relation to the spongy mesophyll and the possible taxonomic significance of the mesophyll has not been reported before. In general, *Ulmus* is characterized by a loose spongy mesophyll and *Celtis* by a compact spongy mesophyll. All leaf specimens were selected at random. Thus, it would appear that any variation resulting from the selection of "sun" versus "shade" leaves would also have been random throughout each genus. Consequently, this variation in leaf mesophyll noted for *Ulmus* and *Celtis* is probably genetic and

not related to environment. However, the use of this character for taxonomic purposes is too uncertain at present and further intensive study is required to establish its value.

Cystoliths were classified as pegged and unpegged. It is obvious from the descriptions of the two that they differ in composition and structure. Pegged cystoliths have a cellulose peg upon which calcium carbonate and silica are deposited, whereas unpegged cystoliths are deposited without a peg and appear to be composed mainly of silica. The taxonomic significance of the presence and distribution of pegged and unpegged cystoliths, as well as of mineral placks, crystals, and mucilage is not clear. All members of Ulmaceae secrete and deposit silica, calcium carbonate, calcium oxalate, and mucilage in varying degrees. The major differences are in the position and form of the deposits. Further study of the secretions and deposits in the leaf and wood of the Ulmaceae is needed. The overall venation pattern and presence or absence of bundle sheaths on terminal tracheary elements seems to be constant within a genus; however, the effects of environment and species variation are not known. The use of such characters in taxonomic treatments may prove valuable later.

One difficulty arising from the investigation of any family which has both ring and diffuse porous species growing in both temperate and tropical regions, is the need for caution in interpreting comparative data between the two groups. Gilbert (1940) has suggested that the ring porous condition is a response to a temperate (seasonal) environment and that resulting evolution has given impetus to development of other so-called "advanced" characters, such as spirals in vessel elements. Others have addressed themselves to this problem and have arrived at basically the same conclusion (Tippo, 1938; Metcalfe & Chalk, 1950). The present study tends to support this contention. Although ring porous species of *Celtis*, *Zelkova*, *Hemiptelea*, and *Ulmus* possess certain associated characters, such as spirals in the vessel elements and relatively shorter fibers and vessels which appear to make them advanced anatomically, they also have scalariform perforation plates and simple plates with vestigial bars, both considered to be primitive features. Diffuse porous species of Ulmaceae and other woody Urticales invariably have simple perforation plates, exclusively. Thus, ring porous species, although possessing some associated advanced characters also have retained certain primitive ones.

Cox (1941) demonstrated in *Celtis* that species of tropical regions are diffuse porous and lack spirals in the vessels while species of temperate areas are ring porous and have spirals in the vessels. *Celtis* species from the present study show the same pattern. In the specimens of *Planera aquatica* examined, two were diffuse porous and one was ring porous. The ring porous specimen was not as markedly ring porous (see "Results" and "Anatomy" portion of "Discussion") as the material of ring porous species of other ulmaceous genera. This condition is probably related to the less pronounced seasonal environment in which *P. aquatica* grows in the southeastern United States. I investigated species of *Quercus* (Fagaceae), which also have ring and diffuse porous members, to deter-

mine if there is any correlation in this genus between porosity and seasonality due to geographical location. Wood specimens of *Quercus* from the Smithsonian Institution wood collection and *Q. virginiana* from Key Largo, Florida, collected by William L. Stern were checked for porosity by means of a hand magnifier. As can be seen from TABLE 5 the temperate

TABLE 5. **Wood porosity of Quercus species arranged in a north-south geographical axis**

SPECIES	R–RING POROUS D–DIFFUSE POROUS	COLLECTION SITE
QUERCUS		
coccinea Muenchh.	R	Brooklyn, N.Y.
alba L.	R	Philadelphia, Pa.
laurifolia Michx.	R	Dismal Swamp, Va.
phellos L.	R	Dismal Swamp, Va.
falcata Michx.	R	Gainesville, Fla.
virginiana Mill.	R	Del Rio, Texas
virginiana	D	Key Largo, Fla.
candicans Née	R–D	Huehuetenango, Guatemala (6,000 ft.)
oleoides Mull.	D	Augustine, British Honduras (2,000 ft.)
copeyensis Mull.	D	Cartago, Costa Rica (8,000 ft.)
baruensis Mull.	R–D	Cerro de Punta, Panama (6,000 ft.)

zone species are all ring porous. However, the tropical and subtropical species are diffuse porous or weakly ring porous. *Quercus virginiana*, like *Planera aquatica*, exhibits both ring and diffuse wood porosity. The only apparent difference in the expression of the porosity appears to depend on the degree of seasonality. The abruptness of seasonal change may be more significant than latitudinal position. *Quercus* species from the latitudinal tropics often inhabit submontane and montane positions where the climate is actually quite cool. The significance of these positions, as far as plant growth is concerned, is the lack of sharp seasonality which does characterize habitats in true temperate zones. For example, in some *Quercus* species from the latitudinal tropics, growth rings themselves are vague, in sharp contrast to their formation in the true temperate zone inhabited by other species of *Quercus*. It appears then, that the genetic potential for the production of ring porous wood occurs in certain species, such as *Planera aquatica* and *Quercus virginiana*, but its expression depends on a seasonal environment.

The solution of the problem of evaluating and comparing characters probably evolved in response to different environmental conditions, tropical *versus* temperate, involves careful evaluation of all characters with conclusions based on study of as much of the phenotype as possible. Also,

within species, even though certain characters appear to be correlated with environment (ring porosity and spirals in temperate regions), other characters remain unaffected and constant and tend to show the relationship between the tropical and temperate elements of these taxa. *Celtis* exemplifies this since it includes species showing ring and diffuse porous wood but having many other anatomical characters in common, such as brochidodromous venation pattern, tight spongy mesophyll, cystoliths in leaves, and heterocellular with transitions to homocellular rays in the secondary xylem. The Ulmaceae as a whole is a good example of this structural-environmental phenomenon in that, even though there are species of temperate and tropical zones (ring porous and diffuse porous), many anatomical characters are held in common by both groups. Consequently, ring porosity and spirals in vessels should not be considered as an advanced anatomical condition in comparisons between taxa of temperate and tropical regions. Instead, ring porosity and spirals should be considered as specializations in Ulmaceae which are correlated with a seasonal temperate environment.

ORDINAL PLACEMENT AND PHYLOGENETIC CONSIDERATIONS

Cronquist, Hutchinson, and Taktahjan all agree that the Urticales should be assigned to a larger category related to and including the Hamamelidales. The only modern phylogenist to disagree is Thorne who places the Urticales in a group having as its progenitor the Malvales. On purely morphological grounds, it is difficult to justify placing the Urticales in a group which has anything but reduced anemophilous flowers; the Malvales complex does not have reduced flowers; the Hamamelidales complex does. TABLE 6 summarizes some external morphological features of both groups. Looking at wood anatomy to help resolve this problem, it is appropriate to quote Bailey (1957): "Thus far, the evolutionary trends in the cambium and xylem of dicotyledons, when considered by themselves, have been most reliable and significant in negations." If we consider the two largest orders on either side of the Urticales (Thorne, Malvales and Rhamnales; Cronquist, Hamamelidales and Juglandales) we find that Urticales are more closely allied in wood anatomy to the latter orders; for example: fibers of Malvaceae and Rhamnaceae have simple pits and perforation plates are exclusively simple, fibers in Hamamelidaceae have distinctly bordered pits and the perforation plates are scalariform, fibers in Juglandaceae have bordered pits and the perforation plates are scalariform to simple (Metcalfe & Chalk, 1950). The urticalean families have fibers with slightly bordered to simple pits and the perforation plates are mostly simple with some scalariform perforation plates in the Ulmaceae. A group with specialized secondary xylem is not likely to give rise to a group with more primitive features. Considering morphological and secondary xylem characters, the systems of Cronquist, Hutchinson, and Takhtajan reflect a more natural placement of the order Urticales.

TABLE 6. **Comparison of morphological features of the largest orders on either side of Urticales**

CRONQUIST (1968)

	HAMAMELIDALES	URTICALES	JUGLANDALES
Growth form	trees-shrubs	trees, shrubs, herbs	trees
Leaf arrangement	alternate	alternate (rarely opposite)	alternate
Calyx parts	4–5	2–8	2–6
Corolla parts	4–5 or absent	absent	absent
Stamens	2–8	2–8	3–40
Carpels	2	1–(2)	2–3
Ovary position	inferior-superior	superior	superior-inferior
Ovules	1 or more	1	2(1)
Ovule position	pendulous	erect-pendulous	erect

THORNE (1968)

	MALVALES	URTICALES	RHAMNALES
Growth form	trees-shrubs	trees-shrubs, herbs	trees, shrubs
Leaf arrangement	alternate	alternate	alternate-opposite
Calyx parts	3–5	2–8	4–5
Corolla parts	3–5	absent	4–5 or absent
Stamens	numerous	2–8	4–5
Carpels	2–10+	1(2)	2–4
Ovary position	superior	superior	superior
Ovules	1–many	1	1–2
Ovule position	pendulous	erect-pendulous	erect-pendulous

Tippo (1938), working with wood anatomy, Bechtel (1921), studying floral morphology, and Lebreton (1965), investigating flavonoids, demonstrated the primitive position of the Ulmaceae within the Urticales. The current anatomical study supports this view.

The Ulmaceae, in respect to all angiosperms, should be considered moderately specialized to specialized in wood anatomy because of the mostly simple perforation plates; short vessel elements; fibers short to medium in length; at least some vessel-end-wall angles of 90°; alternate intervascular pitting; rays homogeneous or with a tendency to homogeneity; storying of vessels, fibers, and rays in some species; and axial parenchyma occurring in groups (apotracheal banded, aliform, confluent). This view is also supported by the specialized condition of the secondary phloem exhibited by sieve tube elements which have slightly oblique to transverse simple sieve plates (Zahur, 1959).

SUMMARY AND CONCLUSIONS

The Ulmaceae is considered to be a natural taxon because of the many leaf and wood characters held in common by its constituent elements. These include the anomocytic stomatal apparatus; bulbous-based unicellular trichomes; similar multicellular hairs; parenchymatous bundle sheaths; presence of silica, calcium carbonate, and mucilage; pinnate venation patterns; relatively short vessel elements, alternate intervascular pitting; mostly simple perforations; relatively short fibers; vascular rays uniseriate, biseriate, and multiseriate, at least some of which are homocellular; and fibers with simple to slightly bordered pits. The tribes of Hutchinson (1967) are more or less distinct anatomically.

This study supports the primitive position of Ulmaceae within the Urticales. Wood anatomy negates the placement of the Urticales near the Malvales and Rhamnales by Thorne (1968) and supports Cronquist (1968) and others in placing the order near the Hamamelidales and Juglandales. In relation to other angiosperm families, Ulmaceae is considered moderately advanced to advanced because of its many specialized wood features, such as simple perforations; short vessel elements; short fibers; vessel-element end-walls of 90°; alternate intervascular pitting; homogeneous rays or a tendency to produce homogeneous rays; storied vessels, fibers, and rays; and apotracheal banded, aliform, and confluent axial parenchyma.

Wood anatomy supports the separation of *Chaetoptelea* from *Ulmus*, as previously noted. *Mirandaceltis*, though differing from *Celtis* in some characters cannot be separated on the basis of wood anatomy.

Gironniera may be divided into two subgenera based on anatomical characters. Subg. GIRONNIERA with large vascular rays and subg. GALUMPITA with smaller vascular rays. Wood and leaf anatomy are insufficient bases on which to separate the subg. GALUMPITA from *Chaetachme*. Subg. GIRONNIERA is reportedly related to *Trema* or *Parasponia*. *Trema* differs in having pegged cystoliths, a multiple epidermis, and acrodromous venation. *Parasponia* differs in leaf anatomy from *Gironniera* in having pegged cystoliths and lacking barbed unicellular hairs. *Trema*, *Parasponia*, and *Gironniera* subg. GIRONNIERA are similar in wood anatomy. Further detailed study of wood and leaf anatomy is warranted to determine variation within species before these *Gironniera* problems can be resolved.

The use of "loose" *versus* "compact" spongy mesophyll and the occurrence and distribution of cystoliths, crystals, mineral placks, and mucilage deserve further study since they might be usefully employed in taxonomic studies. *Ulmus* has a "loose" spongy mesophyll while *Celtis* exhibits a "compact" spongy mesophyll. However, other genera in the Ulmaceae are less consistent. Here too, intensive study on variation within species and effects of environment on production and distribution of mineral deposits and mucilage is needed.

Ring porous woods and associated characters, such as spirals in vessel

elements, are considered to be structural modifications correlated with seasonal environmental conditions, since these conditions occur only in temperate zone species of *Ulmus*, *Celtis*, *Zelkova*, and *Hemiptelea*. *Planera aquatica* can be either ring or diffuse porous. *Planera*, when ring porous, has smaller pores in the early wood than do other ring porous ulmaceous genera; and differs from these genera also in the occurrence of spirals in all vessel elements. The less pronounced ring porosity is probably related to the less marked seasonal nature of the environment of *Planera aquatica* in the southeastern United States. Investigations of porosity in several species of *Quercus* from temperate and tropical regions tend to support this conclusion. Scalariform perforations are reported for the first time in the secondary xylem of species of *Celtis*, *Hemiptelea*, *Zelkova*, *Planera*, and *Ulmus*.

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TABLE 1. Genera of Ulmaceae [a]

GENUS	Leaf: Habit: Tree-T	Leaf: Habit: Shrub-S	Leaf: Arrangement: Alternate-A	Leaf: Arrangement: Opposite-O	Leaf: Margin: Entire-E	Leaf: Margin: Serrate-S	Flowers: Bisexual-B	Flowers: Unisexual-U	Flowers: Sepals, number	Flowers: Stamens, number	Fruit: Samara-S	Fruit: Drupe-D	Fruit: Drupe-like-DL	Fruit: Nutlet with wing-N	Geographical distribution
Tribe ULMEAE															
Chaetoptelea Liebm.	T		A			S	B		5	5			S		Mexico to Panama
Holoptelea Planch.	T		A		E		B		4–8	4–8			S		Asia, Africa
Phyllostylon Capanema ex Benth. & Hook. f.	T		A			S	B		5–8	5–8			S		West Indies to Brazil and Argentina
Planera J. F. Gmel.	T		A			S	B		4–5	4–5			S		Southeastern United States
Ulmus L.	T		A			S	B		4–8	4–8			S		Northern Hemisphere
Tribe CELTEAE															
Ampelocera Klotzsch	T		A		E		B,U		4–5	4–10		D			Tropical America, West Indies
Aphananthe Planch.	T,S		A		S		U		4–5	4–5		D			Eastern Asia, Malaya, Australia, Madagascar
Celtis L.	T,S		A		E–S		B		4–5	4–5		D			Temperate and tropical regions
Chaetachme Planch.	S		A		E		U		5	5		D			Southern Africa, Madagascar

Gironniera Gaudich	T,S	A	E-S	B	5	5	D	Ceylon, Malaya, southern China, Pacific islands
Hemiptelea Planch.	T	A	S	B	4–5	4	N	China
Lozanella Greenman	T	O	S	B	5	5	D	Mexico to Peru
Myrtenaceltis Sharp	T,S	A	S	U	5	5	D	Mexico, Central America
Parasponia Miq.	T,S	A	S	B	5	5	D	Malaya, New Guinea Pacific islands
Phyllostylis Miller ex Baehni	S	A	A	B	4	4–5	D	Peru (Willis, 1966)
Pteroceltis Maxim.	T,S	A	S	U	5	5	DL	Northeast Asia
Trema Lour.	T,S	A	S	U,B	4–5	4–5	D	Tropical and subtropical regions
Zelkova Spach	T	A	S	U	4–5	4–5	DL	Eastern Mediterranean to China and Japan

[a] See references to TABLE 1 on p. 523, 524.

TABLE 4a. Dried wood specimens of Ulmaceae examined [a]

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
AMPELOCERA				
cubensis Griseb.	Bucher 89	Y[d]	Yw16260[e]	Cuba
edentula Kuhlm.		HB	Yw38271	Brazil
edentula		K	USw26186	British Guiana

TABLE 4a. **Dried wood specimens of Ulmaceae examined** *(continued)*

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
glabra Kuhlm.	Milanez *s.n.*		Yw33906	Brazil
hottlei Standl.	Dugand 665	Y	Yw28486	Colombia
APHANANTHE				
aspera Planch.			Yw9313	Japan
philippinensis Planch.			Yw12326	Philippines
CELTIS				
adolphi-friderici Engl.	Vigne 2595	FHO	Yw23576	Gold Coast
asperifolia Merr.			Yw5619	Philippines
australis L.	Chudnoff 52	HUJ	USw22445	Israel
bungeana Blume	Merrill *s.n.*	Fan Mem. Inst.	Yw19955	China
cinnamomea Lindl.	Van de Koppel 5452	Y	Yw22904	Java
crenato-serrata Merr.			Yw2485	Philippines
harperi Horne	A. C. Smith 4637	Y	Yw28285	Fiji
iguanaea (Jacq.) Sarg.			Yw16698	Panama
iguanaea	Stern, Chambers, Dwyer & Ebinger 550	US	Yw54817	Panama
koraiensis Nakai		Fan Mem. Inst.	Yw23015	China
kraussiana Bernh.			Yw1301	Kenya
laevigata Willd.	Oaks, Nogle & Wilson *s.n.*	F	USw22554	Mexico
laevigata	Wiggins & Rollins *s.n.*	DS	USw34190	Mexico

laevigata (as *C. mississippiensis* Bosc)			Aw3217	United States
latifolia Planch.		L	USw23983	New Guinea
lindheimeri Englm.	Nogle *s.n.*		Yw40672	Texas
luzonica Warb.		CLP	USw32756	Philippines
occidentalis L.		MAD	USw18497	Indiana
pacifica Planch.	MacDaniels *s.n.*	CU	Yw25497	Tahiti
pallida Torr.	Detwiler 90	Y	Yw14815	Arizona
paniculata (Endl.) Planch.	St. John 3679	BISH	Yw37320	Hawaii
paniculata var. *multiseriata* R. Br.	Stokes 445	BISH	Yw24294	Austral Islands
philippinensis Blanco		CLP	USw32730	Philippines
reticulata Torr.			Aw3218J	United States
reticulata		F	USw20024	Texas
rigescens Planch.		L	USw24176	New Guinea
ritensis Planch.		BISH	Yw25895	Fiji
schippii Standl.	Kinlock *s.n.*	Y	Yw40282	British Honduras
schippii	Kinlock *s.n.*	Y	Yw40283	British Honduras
sinensis Pers.	Thomson *s.n.*	F	USw20080	Korea
soyauxii Engl.	Vigne 1208	Y	Yw12670	Gold Coast
swartzii Planch.	Ramoncillo 26	Y	Yw9183	Cuba
tala Gill			Yw6212	Argentina
tenuifolia Nutt.	Keth *s.n.*	MAD	USw22919	Virginia
trinervia Lam.	Scarff *s.n.*		Yw32212	Dominican Republic
ugandensis Rendle			Yw13387	Kenya
wightii Planch.			Yw31688	Java
yunnanensis Schneid.	Ying Pe Chang 36	National Central Univ.	Yw48328	China
zenkeri Engl.			Yw47350	Belgian Congo

TABLE 4a. **Dried wood specimens of Ulmaceae examined** (*continued*)

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
CHAETOPTELEA				
mexicana Liebm.	Stern & Chambers 58	Y	USw15582	Panama
mexicana [as *Ulmus mexicana* (Liebm.) Planch.]	Skutch 2040	A	Aw22885	Guatemala
CHAETACHME				
aristata Planch.	Schlieben *s.n.*	B	Yw29375	Africa
microcarpa Warb.			Yw1303	Kenya
GIRONNIERA				
celtidifolia Gaudich.	Waterhouse 149	NY	Yw22860	Melanesia
celtidifolia	A. C. Smith 486	NY	Yw27697	Fiji
cuspidata Kurz			Yw12357	Dutch East Indies
cuspidata	Janssonius 783		Yw31701	Java
nervosa Planch.			Yw12358	Dutch East Indies
nervosa			Yw12359	Dutch East Indies
nitida Benth.			Yw14368	New Caledonia
nitida			Yw13970	New Guinea
subaequalis Planch.		L	Yw20148	New Guinea
HEMIPTELEA				
davidii (Hance) Planch.	Hess *s.n.*	A	Yw35292	Arkansas
HOLOPTELEA				
grandis Mildbr.	Vigne 2504	FHO	Yw23262	Gold Coast

grandis	Donis *s.n.*	BR	USw24390	Congo
integrifolia Planch.		MAD	Yw46153	India
LOZANELLA				
enantiophylla (Donn.-Sm.) Killip & Morton	Stern & Chambers 96	MO	USw16580	Panama
MIRANDACELTIS				
monoica (Hemsl.) Sharp	Sharp 681229	MARY		Mexico
PARASPONIA				
parviflora Miq.	Janssonius *s.n.*		Yw31699	Java
PHYLLOSTYLON				
brasiliensis Cap.	Dugand *s.n.*	Y	Yw23909	Colombia
PLANERA				
aquatica J. F. Gmel.			Yw6699	Florida
aquatica			Yw11169	Florida
aquatica	Wilson *s.n.*	FLAS	USw21789	Florida
PTEROCELTIS				
tatarinowii Maxim.	Ching Wan *s.n.*	Honan Univ.	Yw32019	China
tatarinowii	Ching Wan *s.n.*	Honan Univ.	Yw32143	China
TREMA				
amboinensis Blume	Bryan 2409	BISH	Yw26246	Malaya
angustifolia Planch.	Rahmat Si Boeeca *s.n.*	MICH	USw27851	Sumatra

TABLE 4a. **Dried wood specimens of Ulmaceae examined** *(continued)*

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
bracteolata Blume			Yw3958	Africa
guinensis Priemer	Vigne 1206	MAD	Yw12668	Gold Coast
integerrima (Buer.) Standl.	Acosta-Solís 11986	F	USw20464	Ecuador
lamarckiana (Roem. & Schult.) Blume	Stern & Chambers 227	Y	Yw49407	Florida Keys
micrantha (L.) Blume	Stern 118	Y	Yw49444	Florida Keys
orientalis (L.) Blume		CLP	USw32599	Philippines
vieillardii (Planch.) Benth. & Hook.			Yw13988	New Caledonia
virgata Blume	Tang 215	Fan Mem. Inst.	Yw21827	China
ULMUS				
alata Michx.		A	Aw9054	United States
alata		A	Aw3220	United States
alata		F	Yw26935	Missouri
americana L.		A	Aw3215	United States
americana		MAD	USw18087	Indiana
canescens Melville	Chudnoff 62	HUJ	USw22478	Israel
crassifolia Nutt.		A	Aw3221	United States
glabra Huds.			Yw21586	United States
glabra		US	Yw53493	United States
glabra (as *U. campestris* L.)			Aw9063	Europe
glabra (as *U. campestris*)			Aw9064	Europe
glabra (as *U. campestris*)		FHO	Yw19691	England

hollandica Duroi		FHO	Yw36401	England
hollandica	Clevenger 1274	CLM	USw20605	Ohio
laciniata (Trautv.) Mayr		A	Aw9662	Japan
laciniata		TOFO	USw23712	Japan
laevis Pall.		LE	USw30703	U.S.S.R.
macrocarpa Hance		Fan Mem. Inst.	Yw23012	China
major J. E. Smith		FHO	Yw21587	England
major		FHO	Yw19685	England
minor Mill.		FHO	Yw19687	England
montana With.	Jack 201	A	Aw9078	United States
montana		A	Yw9079	England
montana		FHO	Yw19686	England
nitens Moench		FHO	Yw19689	England
parvifolia Jacq.	Kanehira 92	FHO	Yw6493	Formosa
plotii Druce		FHO	Yw50005	England
procera Salisb.	Clevenger 1272	CLM	USw20603	Ohio
procera	Clevenger 1261	CLM	USw20604	Ohio
pumila L.	Hicock *s.n.*	A	Yw40235	Connecticut
rubra Muhl. (as *U. fulva* Michx.)		A	Aw9069	United States
rubra (as *U. fulva*)		A	Aw3214	United States
scabra Mill.		DOZ	Yw23180	Poland
serotina Sarg.		A	Aw9082	Illinois
serotina	E. S. Harrar 8474	DUKE	Yw43454	United States
sieboldii Daveau	Pilcher 124		USw21177	Japan
stricta Lindl.		FHO	Yw19690	England
suberosa Ehrh.		DOZ	Yw23154	Poland
thomasii Sarg.	Schmidt *s.n.*	MAD	USw23450	United States
uyematsii Hayata	Fiyioka *s.n.*	TI	Yw24060	Formosa

TABLE 4a. **Dried wood specimens of Ulmaceae examined** *(continued)*

SPECIES	COLLECTOR	HERBARIUM VOUCHER [b]	WOOD COLLECTION [c]	ORIGIN
wallichii Planch.		Pakistan Forest Research Institute	Yw49654	Pakistan
ZELKOVA				
keakii (Sieb.) Maxim.			Yw2003	Japan
serrata (Thunb.) Nakai		TOFO	USw23713	Japan

[a] See reference to TABLE 4a on p. 532.
[b] Abbreviations follow those recommended by Lanjouw & Stafleu (1964) in *Index Herbariorum*.
[c] Abbreviations follow those recommended by Stern (1967) in *Index Xylariorum*.
[d] Y refers to the herbarium and Yw to the xylarium formerly located at the Yale University School of Forestry, but now housed at the U.S. Forest Products Laboratory, Madison, Wisconsin, as the Samuel James Record Memorial Collection.

TABLE 4b. **Dried leaf specimens of Ulmaceae examined** [a,b]

SPECIES	COLLECTOR	ORIGIN
AMPELOCERA		
cubensis Griseb.	Ekman 9470	Cuba
edentula Kuhlm.	Ducke 1736	Brazil
hottlei Standl.	Ll. Williams 9497	Mexico
APHANANTHE		
aspera Planch.	Chiao 2935	China
philippinensis Planch.	Edaño 26773	Luzon
CELTIS		
bungeana Blume	Wilson 10459	Korea
caudata Hance	Callado 9592	Mexico
iguanaea (Jacq.) Sarg.	Standley 1500	Mexico
laevigata Willd.	Thieret 16497	Louisiana
laevigata var. *texana* (Scheele) Sarg.	Lodewyks 382a	Missouri
occidentalis L.	Allard 7931	Virginia
occidentalis var. *crassifolia* (Lam.) A. Gray	Peck *s.n.*	New York
pallida Torr.	Killip 32729	Arizona
philippinensis Blanco	Conteras 23396	Philippines
pubescens Granat.	Pickel 1177	Brazil
pumila Pursh	Harbison *s.n.*	Virginia
reticulata Torr.	Johnson 8580	Arizona
reticulata (as *C. douglasii* Planch.)	Jahn 8449	Washington
schippii Standl.	Little 6216	Ecuador
sinensis Pers.	Lau 388	China
spinosa Ruiz	Jorgenson 3853	Paraguay
tenuifolia Nutt.	Fernald & Long 13326	Virginia
tenuifolia	Terrell & Barclay 3373	Alabama
triflora Lam.	Smith & Klein 11162	Brazil
trinervia Lam.	Webster 3679	Cuba
CHAETACHME		
aristata Planch.	Zenker & Haudz 430	French Cameroons
microcarpa Rendle	Piemeisel & Kephart 21	Kenya
CHAETOPTELEA		
mexicana Liebm.	Standley 20002	Mexico
GIRONNIERA		
celtidifolia Gaudich.	Beer 7082	Solomon Islands
cuspidata Kurz	Lei 831	China
nervosa Planch.	Low & Motan 94530	Malay Peninsula

TABLE 4b. **Dried leaf specimens of Ulmaceae examined** [a,b] (*continued*)

SPECIES	COLLECTOR	ORIGIN
nitida Benth.	Taan 1629	Hong Kong
parvifolia Planch.	King 5369	Malay Peninsula
reticulata Thw.	Piolane 10768	South Vietnam
HEMIPTELEA		
davidii (Hance) Planch.	Dorsett 564	China
HOLOPTELEA		
integrifolia Planch.	Choudhury 108	India
LOZANELLA		
enantiophylla (Donn.-Sm.) Killip & Morton	Hinton 14286	Mexico
MIRANDACELTIS		
monoica (Hemsl.) Sharp	Andrle 51	Mexico
monoica	Andrle 103	Mexico
PARASPONIA		
andersonii Miq.	Baumann 6138	New Caledonia
PHYLLOSTYLON		
brasiliensis Cap.	Kuhlmann 17991	Brazil
rhamnoides Taub.	Dugand 5511	Colombia
PLANERA		
aquatica J. F. Gmel.	Palmer 15124	Florida
PTEROCELTIS		
tatarinowii Maxim.	Chiao 3085	China
TREMA		
amboinensis Blume	Santos 4656	Philippines
canescens Blume	Garnier 688	Nicaragua
lamarckiana (Beur.) Standl.	Small 8078	Florida
micrantha (L.) Blume	Dressler 1660	Mexico
orientalis (L.) Blume	Henry 12189A	China
ULMUS		
alata Michx.	Moore & Horton 6740	Louisiana
americana L.	Hoy 521	New York
carpinifolia Gleditsch	Harrison 10593	Utah
crassifolia Nutt.	Palmer 24050	Oklahoma
glabra Huds.	Norman *s.n.*	Spain
glabra (as *U. campestris* L.)	Baenitz *s.n.*	Poland
hollandica Duroi	Sonnobree 3523	Belgium

TABLE 4b. **Dried leaf specimens of Ulmaceae examined** [a,b] (*continued*)

SPECIES	COLLECTOR	ORIGIN
laevis Pall.	US1750849	Poland
minor Mill.	David 3A	England
montana With.	Paulsen *s.n.*	Denmark
parvifolia Jacq.	Howell 26645	California
parvifolia	Terakawa 136	Japan
pumila L.	Purdon 1048	China
rubra Muhl. (as *U. fulva* Michx.)	Humphrey *s.n.*	Wisconsin
rubra (as *U. fulva*)	Sheldon *s.n.*	Minnesota
serotina Sarg.	Biltmore Herb. 3634	Georgia
thomasii Sarg.	Toumey *s.n.*	Connecticut
ZELKOVA		
carpinifolia (Pall.) Koch	Sudworth *s.n.*	District of Columbia
serrata Makino	Sudworth *s.n.*	District of Columbia
sinica Schneid.	Pei 3077	China

[a] All dried leaf specimens obtained from United States National Herbarium, Smithsonian Institution, Washington, D.C.

[b] See reference to TABLE 4b on p. 532.

TABLE 4c. Preserved leaf and wood specimens of Ulmaceae examined [a,b]

SPECIES	HERBARIUM VOUCHER	RANGE [c]
CELTIS		
bungeana Blume	A643–53	Central and northern China, Manchuria, and Korea
jessoensis Koidz.	A7532	Korea and Japan
laevigata Willd.	A112–54–A	Southern Indiana and Illinois to Texas and Florida
laevigata var. *smallii* (Beadle) Sarg.	A1165	North Carolina and Tennessee to Georgia and Alabama
occidentalis L.	A36937B	Quebec to Manitoba, south to North Carolina, Alabama, and Kansas
occidentalis var. *cordata* Pers.	A15954A	United States
pumila Pursh	A12999B	New Jersey to Florida, west to Kansas, Colorado, and Utah
reticulata Torr.	A587–56A	Colorado and Texas to Washington and southern California
reticulata (as *C. douglasii* Planch.)	A21779	Colorado and Texas to Washington and southern California
tournefortii Lam.	A593–56B	Mediterranean region
HEMIPTELEA		
davidii (Hance) Planch.	A5283	Northern China, Manchuria, and Korea
TREMA		
lamarckiana (Roem. & Schult.) Blume	MARY, Stern 2660	Florida Keys and southern Florida
micrantha (L.) Blume	MARY, Stern 2661	Florida Keys and southern Florida
ULMUS		
americana L.	MARY, Sweitzer, *s.n.*	Newfoundland to Florida and west to Rocky Mountains
carpinifolia Gleditsch	A17883	Europe, northern Africa, and western Asia
carpinifolia var. *suberosa* (Moench) Rehd.	A17880	Europe
glabra Huds.	A17143	Northern and central Europe, western Asia

hollandica Mill.	A17921	Europe
laevis Pall.	A17910	Europe, western Asia
procera Salisb.	A90–4–38	England, western and southern Europe
pumila L.	A15936	Eastern Siberia, northern China, and Turkestan
pumila var. *arborea* Litv.	A15939	Turkestan
rubra Michx.	A21966A	Eastern United States, west to Texas, Oklahoma, Nebraska, North Dakota, and north to Quebec
thomasii Sarg.	A17925F	Quebec to Tennessee, west to Nebraska

[a] All specimens were collected at the Arnold Arboretum, Boston, Massachusetts, except those with MARY herbarium vouchers, where the collector's name is listed.

[b] See reference to TABLE 4c on p. 532.

[c] Ranges were taken from Planchon (1873), Rehder (1940), L. H. Bailey (1949), and Little (1953).

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 16. THE FLOWERING CYCLE AND AN INTERPRETATION OF ITS SEASONALITY

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THIS STUDY WAS UNDERTAKEN as a part of the investigation of the dynamics of a forest located on Pico del Oeste, in the Sierra de Luquillo of Puerto Rico.[1] Pico del Oeste is the third highest peak (1050 meters) of the Luquillo formation and is located slightly northwest of Pico del Este. The summit is covered by a dense stand of trees and shrubs of small stature which form a peculiar vegetation type known as the elfin forest. The plants are evergreen and usually festooned with flowering and non-flowering epiphytes. While preceding papers in this series have stressed the multi-faceted peculiarities of the elfin forest, this paper is intended to stress one aspect which the elfin forest has in common with all other forests — the reproductive cycle.

There are few organized records of flowering times for tropical plant species and those which exist have been in large part compiled by monographers or floristic workers, largely on the basis of herbarium specimens. The elfin forest study seemed therefore to be a unique opportunity to obtain reliable flowering and fruiting data. These data, particularly the resulting patterns of flowering and fruiting, have been useful in helping to focus attention on a number of questions such as an interpretation of seasonality, responses to seasonality, comparative studies with lowland floras, and the relative roles of vegetative and sexual reproduction. Only after some of these questions were explored was it possible to consider properly the origin of the floristic elements of the Pico del Oeste elfin forest. The "flora" is a small one and was found to consist of 15 species of Monocotyledons and 40 species of Dicotyledons plus the non-flowering species (see Howard, 1968; Fulford *et al.*, 1970; and Foerster 1971 for details of the latter). According to Howard (1968) approximately 14 percent of the monocots and 55 percent of the dicots are endemic to Puerto Rico. A general endemism for the plants of the Sierra de Luquillo has been suggested as about 18 percent. Although the species of Pico del Oeste show a high percentage of endemism (i.e., they are restricted to Puerto Rico) I do not believe any species is restricted solely to the elfin forest formation. A general statement that the species components of this elfin forest also occur as a part of the flora at somewhat lower altitudes seems pertinent. The Pico flora may be considered as derived from a portion of the flora found at lower elevations; the reason for the small number of flowering

[1] This study was partially supported by a grant from the National Science Foundation (GB-3975) to Dr. R. A. Howard, principal investigator.

species being that few of the species are adapted to the prevailing climatic conditions of the elfin forest.

FLOWERING

Preliminary transects of the site were made in the fall of 1965 when tentative identifications were obtained from representative collections. These determinations formed the basis of a checklist of the plants of Pico del Oeste and representative specimens were labelled both at canopy and ground level (for details see Howard, 1968). This labelling proved to be of particular importance because of the number and variety of personnel who were to be involved in the maintenance of the records. The "flora" could be learned in a relatively short period and the number of misidentifications was kept to a minimum. Weekly records of flowering and fruiting were kept from February 1966 to January 1968 inclusive, and the completeness of the record attests to the faithfulness of all persons concerned.

The weekly flowering and fruiting records were combined into a single cumulative monthly record which is presented in TABLE 1. The records are restricted to the plants growing on the site and do not include individuals of the same species growing at lower altitudes or in other geographic localities. The scoring was on the basis of all or none. Quantity was not scored inasmuch as few individual observers had previous experience with the species under study and had no point of reference in this regard.

There are a few abnormalities in the record which lead me to the conclusion that the two-year record, while useful, does not give an accurate indication of the sexual reproductive cycles of the plants of Pico del Oeste. Extended observations would tend to show more variability than is now shown for some of the species. The flowering record must be considered to be more accurate than that for fruiting as most observers had the tendency to begin scoring a plant in fruit as soon as fruit development became apparent. In many instances, however, mature fruit did not develop during the course of the observations. There are a few additional anomalies in the flowering record which must be commented upon. The record for *Andropogon bicornis* is incomplete as it was represented by a single clump which was destroyed accidentally very early in the study period. *Arthrostylidium sarmentosum* is known in flower only from one previous collection, and because of its very reduced inflorescence may have been overlooked if and when it did flower. *Rajania cordata* failed to flower on the study site, although it flowers conspicuously at lower altitudes. *Trichilia pallida* and *Hillia parasitica* were represented by juvenile plants only and may not be regular members of the community. *Renealmia antillarum* and *Lobelia portoricensis* were each represented by a single large specimen but as they both flowered continuously no record gap exists. In one species, *Vriesea sintenisii*, the flowering record as given in TABLE 1 may be exaggerated. This *Vriesea* is few-flowered and the white flowers last for a few days only. In contrast the inflorescences are long-persistent

TABLE 1. **Cumulative monthly flowering and fruiting records for Pico del Oeste** [1]

FAMILY and SPECIES	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
GRAMINEAE												
Andropogon bicornis		+*										
Arthrostylidium sarmentosum												
Ichnanthus pallens	+*	+*	+*	+*	+*	+*	+*		*			*
Isachne angustifolia		+*	+*	+*	+*	+*	+*	+*	*	*		+*
CYPERACEAE												
Carex polystachya	*		+*	+*	+*	+*	+*	+*	+*	*	*	*
Eleocharis yunquensis	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Scleria secans	+*	*	+*	+*	+*	+*	+*	+*	+*	*	+*	
PALMAE												
Prestoea montana	+*	+*	*	*	*	+*	+*	+*	+*	+*	+*	*
ARACEAE												
Anthurium dominicense	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
BROMELIACEAE												
Guzmania berteroniana	*		*	*		+	+*	+*	+*		+	+*
Vriesea sintenisii	*	+*	*	+*	+*	+*	+*	+*	+*	+*	+*	*
DIOSCOREACEAE												
Rajania cordata												
ZINGIBERACEAE												
Renealmia antillarum	+*	+	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
ORCHIDACEAE												
Brachionidium ciliolatum [2]	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	*
Dilomilis montana	+	+*	+*	+*	+*	*	+					+*

PIPERACEAE												
Peperomia emarginella						+	+	+	+*	+*	+*	
Peperomia hernandiifolia	+*	+*	+*		+*	+*	+	+*	+*	+*	+*	+*
CHLORANTHACEAE												
Hedyosmum arborescens	+	+	+*	+*	+	+*	+*	*	+*	+		
MORACEAE												
Cecropia peltata	+			+	+*	+*	*				+	+
URTICACEAE												
Pilea krugii			+*	+*	+*	+*	+*	+*	+*	+*	+*	
Pilea yunquensis		+	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
LAURACEAE												
Ocotea spathulata	*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
MELIACEAE												
Trichilia pallida												
AQUIFOLIACEAE												
Ilex sintenisii	*			+	+*	+*	+*	+*	+*	+*	+*	+*
CELASTRACEAE												
Torralbasia cuneifolia							+		+		+	
OCHNACEAE												
Sauvagesia erecta	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
MARCGRAVIACEAE												
Marcgravia sintenisii	+*	*	*	+*	*	+*	+*	+	+*	+*	+*	+*
THEACEAE												
Cleyera albopunctata	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*

TABLE 1. Cumulative monthly flowering and fruiting records for Pico del Oeste (*continued*)

FAMILY and SPECIES	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
GUTTIFERAE												
Clusia grisebachiana			*				+*			+		
BEGONIACEAE												
Begonia decandra	+		+*	+	+	+	+*	+*	+	+	+*	+
MYRTACEAE												
Calyptranthes krugii	*	*			+	+	+	+	+*	+*	+*	*
Eugenia borinquensis	+*					+	+	+*	+*	+*	+*	+*
MELASTOMATACEAE												
Calycogonium squamulosum							+			+	+	+
Mecranium amygdalinum	+						+	+			+*	+*
Miconia foveolata	+*	+	+*	+*	+*	+*	+*	+*	+*	+*	*	+*
Miconia pachyphylla	+	+	+*	+*	+*	+*	+*	*	*	+*	*	
Miconia sintenisii	+	+*	+*	*	*				+*	+*		+
ERICACEAE												
Gonocalyx portoricensis	+	+	+*	+*	+*	+*	+*	+*	+*	+	+	+*
Hornemannia racemosa		+	+	+*		+*	+*	+*	+*	+	+*	
MYRSINACEAE												
Ardisia luquillensis	+*	+*	*	+*	*	*	+*	*	+	+*	+*	+*
Cymbianthopsis sintenisii[3]	*					+	+	+	+*	+*	+*	+*
Wallenia yunquensis	*	*	+*	+*	+*	+*	+*	+	+*	+*	+*	+*
SAPOTACEAE												
Micropholis garciniifolia	+*		+			+	+*	+*	+*	+*	*	

SYMPLOCACEAE												
Symplocos micrantha	+		+				+					
OLEACEAE												
Haenianthus salicifolius	+*									+*	+*	
CONVOLVULACEAE												
Ipomoea repanda	+*									+	+	+
BIGNONIACEAE												
Tabebuia rigida	+	+	+	+	+	+	+	+	+	+	+	+
GESNERIACEAE												
Alloplectus ambiguus	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
Gesneria sintenisii	+*	*	+*							+	+*	+*
ACANTHACEAE												
Justicia martinsoniana	+*	+*	+*	+*	+*	+*	+*	+		+	+	+*
RUBIACEAE												
Hillia parasitica												
Psychotria berteriana	+*	+	+*	+*	+*	+*	+*	*	*	+	+	+
Psychotria guadalupensis	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
CAMPANULACEAE												
Lobelia portoricensis	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*	+*
COMPOSITAE												
Mikania pachyphylla		+	+*	+*	+*	+*	+*					

[1] Plus sign (+) = flowering; asterisk (*) = fruiting.

[2] *Brachionidium ciliolatum* Garay (Jour. Arnold Arb. 50: 464. 1969) has been treated as *B. parvum* Cogn. in previous papers in this series.

[3] *Cymbianthopsis sintenisii* (Urb.) Lundell (Wrightia 4: 68. 1968) has been treated as *Grammadena sintenisii* (Urb.) Mez in previous papers in this series.

and we are inclined to believe that they were incorrectly scored as flowering.

TABLE 1 has several additional shortcomings because it is a cumulative record. In the case of *Haenianthus salicifolius* (Oleaceae) flowering was not observed until late in 1967. When in flower and fruit this small tree is quite spectacular and is unlikely to be missed. It is safe to assume that it did not flower in 1966. Therefore, the records show when a species flowered but cannot be used to predict that any individual species will be in flower in a particular month in any given year. A second type of difficulty is based on the all-or-none scoring of flowering and fruiting. A good example is supplied by *Dilomilis montana* (Orchidaceae) which flowers for seven months of the year. It does reach a flowering peak in January and February, a fact that is not noted in the cumulative record (and that could be established only at the end of the observation period).

The records which were compiled from Pico del Oeste are by no means comprehensive and in order to determine the relative degree of accuracy additional flowering records for these species were compiled from herbarium material from the entire island of Puerto Rico. The additional monthly flowering records are as follows:

Andropogon bicornis: April, October.
Isachne angustifolia: January.
Scleria secans: October.
Prestoea montana: March, April, May, December.
Rajania cordata: January, April, May, June, July, October, November, December.
Dilomilis montana: September, October, November.
Peperomia hernandiifolia: April.
Hedyosmum arborescens: November.
Cecropia peltata: February, March, July, August, October.
Pilea yunquensis: January.
Ocotea spathulata: January.
Trichilia pallida: January, April, May, June, July, September, November.
Ilex sintenisii: March.
Torralbasia cuneifolia: August.
Marcgravia sintenisii: February.
Clusia grisebachiana: September.
Begonia decandra: February.
Calyptranthes krugii: April.
Calycogonium squamulosum: January, August.
Mecranium amygdalinum: February, May, June.
Miconia pachyphylla: September.
Hornemannia racemosa: January, December.
Micropholis garciniifolia: February, April, May, November, December.
Ipomoea repanda: June, September.
Hillia parasitica: All months of the year.

The cumulative monthly flowering record for the plants on Pico del Oeste is given in FIGURE 1. It is presented against the background of the total cumulative records from all of Puerto Rico. In general, the pattern

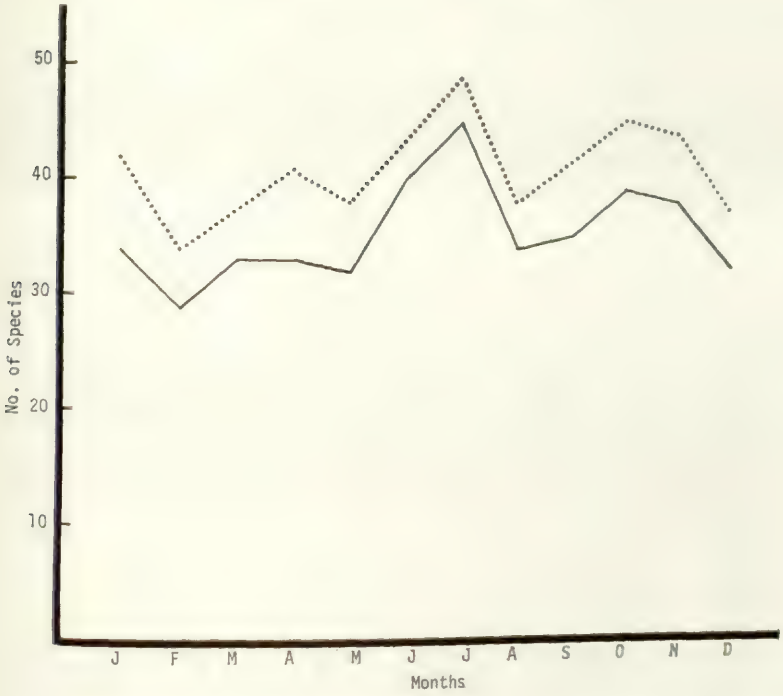

FIGURE 1. Cumulative monthly flowering record of the plants of Pico del Oeste. Solid line record is based on observations and herbarium records from the Pico only. Dotted line record is based on all available data sources of the Pico species from all of Puerto Rico.

for both is similar and we believe this indicates that our observations are relatively accurate and continued observations could be expected only to add some months of flowering for individual species. It appears as though the overall pattern would remain static.

The most striking individual feature is the flowering peak (45 species) which is attained in the month of July. This may provide some practical advice for future collectors in the elfin forest, namely, they may collect most effectively, in terms of the number of species in flower, in July. An equally interesting situation is found in the month of October when a secondary flowering peak of 39 species is found.

The question as to whether chromosome number plays any role in the length of flowering must be considered since ploidy level has been correlated by some with survival under extreme environmental conditions. The term survival should imply the ability to reproduce in one form or another. Reduction of the available chromosome counts to the haploid level (Nevling, 1969) and plotting the potential months in flower for each species with a particular haploid number is not helpful.

$n = 26$ — 7 months	$n = 15$ — 6, 12 months
25 — 0	14 — 11, 11
24 — 12	13 — 0
23 — 7	12 — 3, 5, 9, 12, 12, 12
22 — 12	11 — 0
21 — 10, 10	10 — 0
20 — 3, 6, 7, 10	9 — 0
19 — 11, 12	8 — 10, 10
18 — 8, 12	7 — 5, 12
17 — 9, 11	6 — 0
16 — 0	5 — 9

There appears to be no relationship between flowering duration and absolute chromosome number. The data for ploidy level are too limited to evaluate, as most of the counts reported previously remain all that is available for a genus.

By plotting the flowering records (FIGURE 2) on the basis of Mono-

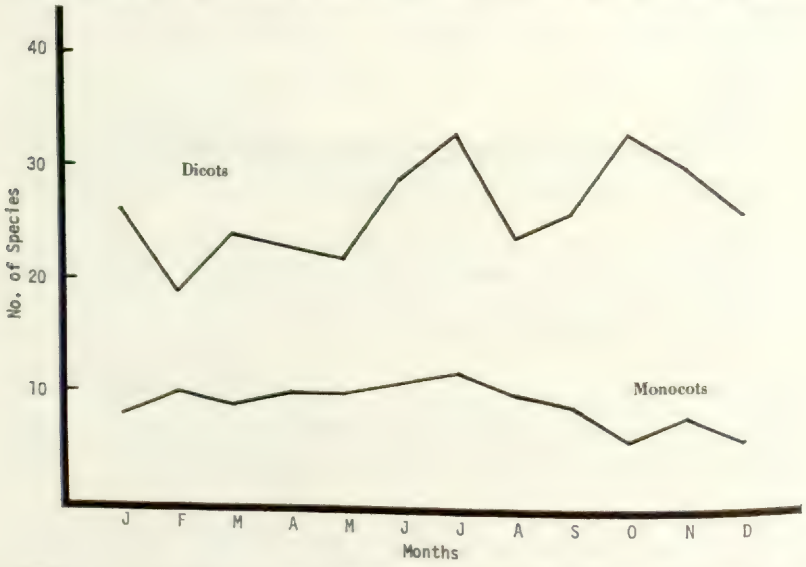

FIGURE 2. Cumulative monthly flowering records of the Dicotyledons and Monocotyledons of Pico del Oeste.

cotyledons *vs.* Dicotyledons the difference between the flowering peaks of July and October is sharpened. The general pattern in the monocots is for a gradual increase in the number of species flowering from January through July, with a decrease towards the end of the year. Interestingly, the lowest flowering level is found in October. The Dicotyledons, in contrast, follow a strong bimodal flowering curve. The primary peak is in July followed by a precipitous drop in flowering in August. The overall peak in July is due to the coincidence of the flowering peaks of both the

Monocotyledons and Dicotyledons. The secondary peak, in October, which was also reflected in the overall flowering pattern, is due to the Dicotyledons alone as the Monocotyledons reach their low point during the month.

Another informative way of presenting the flowering record is by habit (FIGURE 3). I have arbitrarily sorted the species into five categories: trees, shrubs, climbers, and herbs with the latter subdivided into terrestrial and epiphytic herbs. In some instances a species is referable to more than

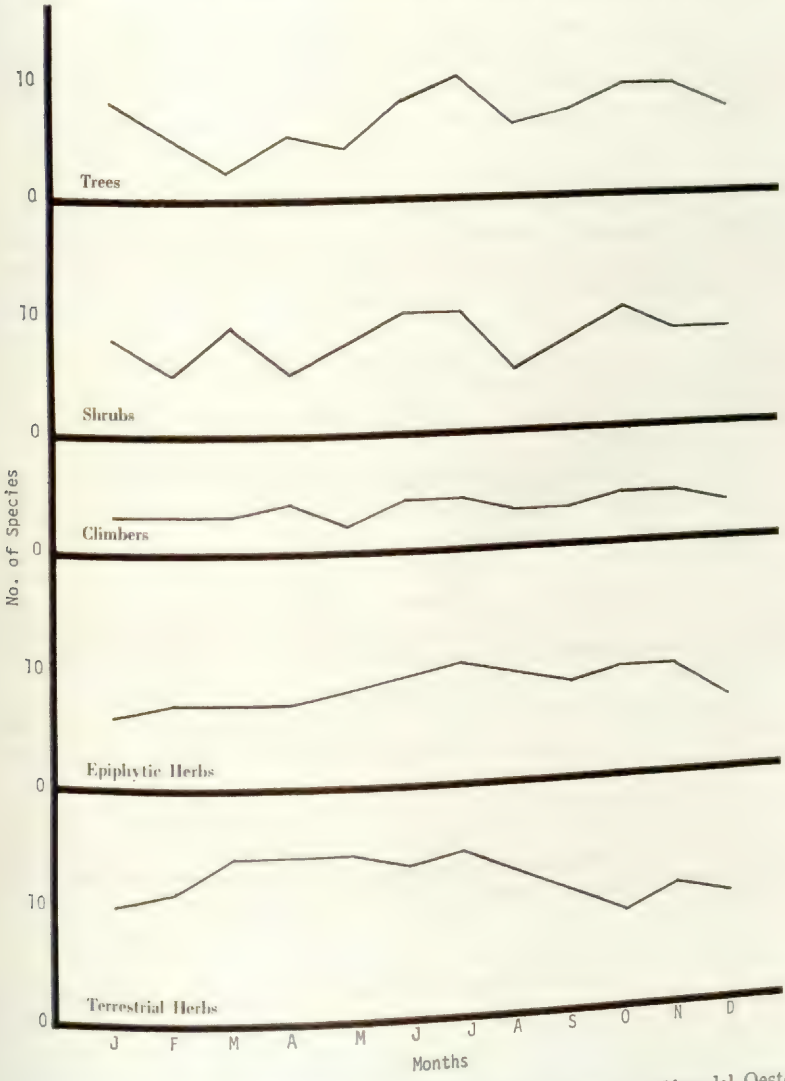

FIGURE 3. Cumulative monthly flowering records of plants of Pico del Oeste divided according to habit and habitat preference: trees; shrubs; climbers; epiphytic herbs; terrestrial herbs.

one category, *Dilomilis montana* is found both epiphytically and terrestrially and consequently is scored in both categories. Some differences are apparent in the flowering behavior of the separate groupings.

The record for trees shows a remarkable drop in flowering beginning with the month of January and ending in the month of March; this is followed by a gradual rise with a slight peak in April. There is a decrease in May and a gradual rise to a high in the month of July. Then flowering drops off sharply and gradually goes to a secondary high in the months of October and November. The pattern for the shrub flowering is somewhat more complex, with a sharp decrease in January and February and a rather interesting increase in the month of March followed by decrease in April and a gradual rise to high months for June and July followed by decrease in August and an increase to the month of October. The high months are June, July, and October and in general this pattern follows that for trees. There was some question in the results for trees of the tertiary peak found in April. This tertiary peak also seems to be found in the shrubs but one month earlier, and so may not be an artifact of observation but rather a record of some importance. The pattern for the climbers is not especially revealing because of the small number of species. Otherwise, the high months are April, June, July, October, and November with some depression in the months of May, August, September, and December and the early part of the year. In general it does follow the flowering pattern found in both trees and shrubs.

The flowering pattern of the herbaceous species can be understood only by distinguishing the epiphytic from the terrestrial components and plotting them separately. The flowering pattern for the epiphytic herbs parallels that of the trees and shrubs except that it is missing the tertiary flowering peak found early in the year. There is a gradual increase in species in flower for the month of April, culminating in July, followed by decreases in August and September, the secondary peak being attained in October and November. The pattern for the terrestrial herbs is in striking contrast with that presented for the other life forms. Flowering rises rather rapidly from January and a plateau is reached in the months of March, April, and May with a slight depression in June, and another high peak in July, followed by severe depression of the flowering species through October, following which time there is a slight rise in the month of November. The bulk of the flowering seems to be concentrated in the first seven months of the year. This is a different pattern from other habit types, with the exception of one of the high months being July, and with a slight restoration of flowering in the month of November.

One of the unsuccessful aspects of the Pico del Oeste study was an attempt to collect and identify the pollinators on the site. The most conspicuous insect observed is a wasp, *Polistes crinitus* Felton ssp. *americanus* Fab. Large numbers were seen hovering over the canopy minutes after the Pico became insolated. Previous reports attributed the presence of this wasp species on the summits of the Luquillo mountains to sexual flights or to strong updrafts which blow the wasps uphill. Both explanations are

invalid and the wasps are regular members of the peak biological assemblage but they do not appear to have a role in pollination. The failure to identify pollinators was not due to lack of diligence on the part of the observers but to an apparent lack of pollinators. That is not to say that the insect assemblage on the peak is small as there is a considerable array of phytophagous insects present and active. In only one instance was a definite pollinator correlated with a specific plant and that was the case of *Prestoea montana*, pollinated by a species of bee flies (*Bombylius*). Although this may have been the most disappointing aspect of the study it may explain, in part, the extraordinarily low percentage of fruit set. Those plants which depend on an outbreeding system would be seriously affected by lack of pollinators. This lack may be due to the great frequency of rainfall and consistently high humidity which dilutes nectar concentration and decreases attractiveness. In spite of being unable to identify the pollinators it is possible to speculate with some assurance upon the possible pollinators for most of the plant species. This can be done by considering the pollination syndrome for each individual species. In FIGURE 4, I have attempted to separate the flowering records of those species which

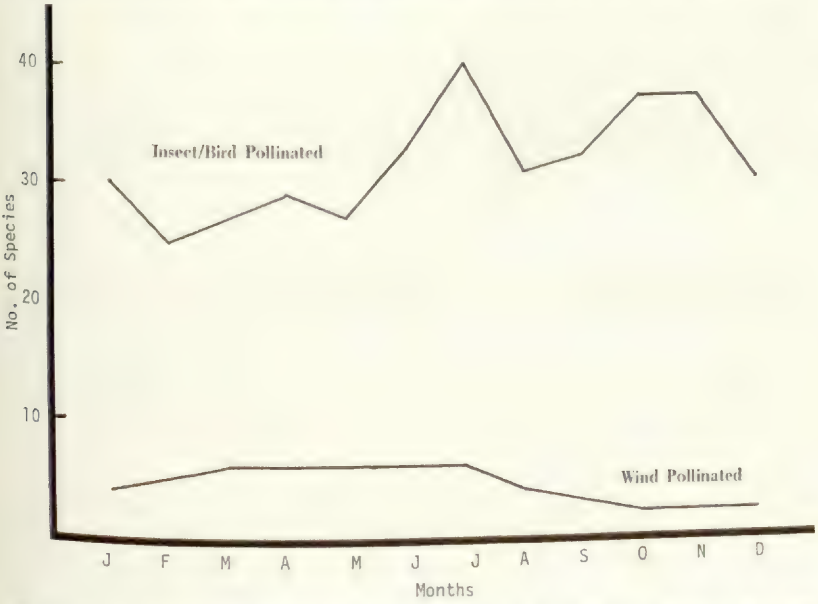

FIGURE 4. Cumulative monthly flowering records from Pico del Oeste plotted as species with bird/insect pollination syndrome *vs.* species with wind pollination syndrome.

are projected as plants which have a bird- or insect-pollination syndrome from those which have a wind-pollination syndrome. Although it is usually easy to distinguish between bird- and insect-pollinated species this distinction was rather vague in the possible bird-pollinated species so it seemed

appropriate to present these as a single plot. Janzen (1967) has reported that the activity of insect pollinators peaks during the dry season while the activity of bird pollinators peaks during the wet season. The flowering record for the bird-insect pollinated species is very similar to that for the Dicotyledons, with a primary peak in July, a secondary peak in October–November, and a tertiary peak in the month of April. The wind-pollinated species are at a tremendous disadvantage in the climatic regime of the Pico because of rainfall. With high rainfall distributed throughout the year good opportunities for pollen transport are rare indeed. Not only is direct rainfall, which almost immediately cleans the air of pollen, a significant problem, but also the accompanying long-term periods of high humidity are influential. During such periods of high humidity the individual florets of wind-pollinated species do not have the opportunity to become dry and shed pollen in the normal manner. Ogle (1970) has reported that petroleum jelly coated slides exposed at El Verde, Puerto Rico, yielded no results.[2] We ran a similar experiment using six Durham gravity pollen samplers and found a considerable number of spores, pollen grains, and insect parts but it has not been possible to bring this portion of the study to a conclusion. The actual number of projected wind-pollinated species is small within the total flora and this is not unexpected as the percentage of wind-pollinated species in the tropics is much lower in general than that which one encounters in temperate regions. The actual plot of the flowering record is very reminiscent of that shown by the terrestrial herbaceous herbs and in fact the two should correspond closely because most of the wind-pollinated species are terrestrial herbs. There is a gradual rise in flowering from January to April followed by a long peak plateau, May to July. This plateau is followed by a general decrease until October when a low plateau extending through December is reached.

The flowering period of many plants of temperate regions is controlled by a daylength response. Short-day and long-day plants are well known and this precise response to various regimes is exploited by flower growers in order to bring certain crops such as *Chrysanthemum* or *Euphorbia pulcherrima* into flower at the proper festive season. In contrast, many plant species of the tropics do not appear to use day-length as the marker for floral initiation. This may be partially because of the lessening difference between the longest and shortest day of the year as one approaches the equator. In Puerto Rico this difference still amounts to more than two hours over the year. We are more accustomed to correlate flowering in the tropics with dry/wet seasonality. Flowering times of tropical plants often are expressed in terms such as "at the onset of the rainy season" or during the "dry season" and not necessarily in terms of months of the year.

The plants of Pico del Oeste are in a rather peculiar situation because

[2] Strictly as an aside, Ogle, in her discussion of results, mentions that among the important but unidentified components were pollen grains of a Rutaceous type. I believe this is a *lapsus* for Rubiaceous type. Further, she indicates that *Casuarina* was first introduced to the island in 1923, although there is an herbarium specimen, from cultivation in Ponce (*Sintenis 4872* (GH)), dated 1886.

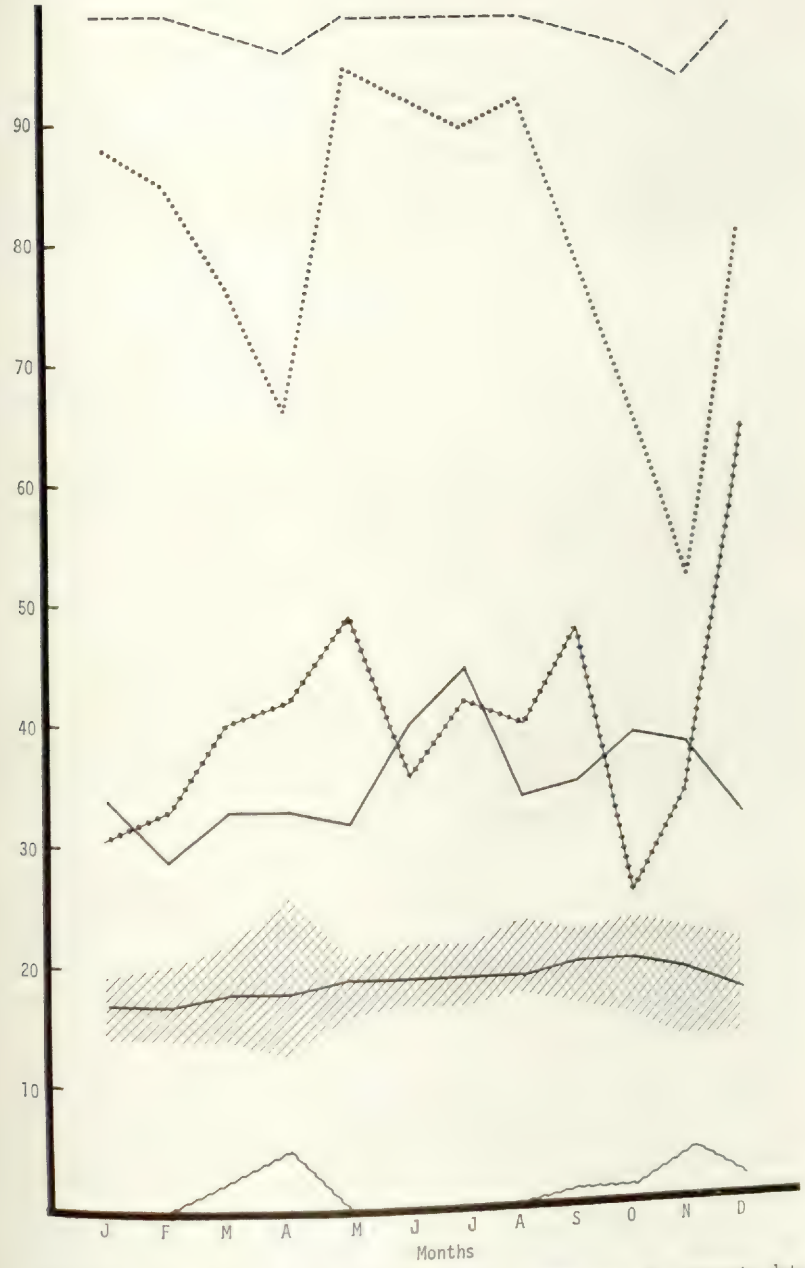

FIGURE 5. Flowering data of Pico del Oeste correlated with climatic data. Dashed line = mean minimum relative humidity (in percent); dotted line = percentage of hours of 100% humidity; solid line with diamonds = rainfall (in cm.); solid line = flowering (in number of species); solid line within shaded area = mean temperature (in C°); shaded area = absolute maximum and minimum temperature differential (in C°); wavy line = number of days with no rainfall.

they are in a tropical area but the microclimate is such that a dry/wet seasonality does not seem to be well marked (especially as the month with the lowest rainfall has 26 cm. of rain). The question of identifying the physiological trigger of the flowering response in these plants has proven to be a difficult one.

The flowering record has been plotted with several environmental variables (FIGURE 5). All of the environmental data were supplied by the National Center for Atmospheric Research (NCAR) except those for total rainfall which is based on data generated independently by the various observers from Harvard University. The median air temperature at canopy level gradually rises from a low in December, January, and February to a high in September and October. This change is slight, the difference between the high and the low being only three degrees centigrade. The absolute maximum and minimum temperatures have been plotted as well. The greatest difference between night (low) and day (high) temperatures is found in the month of April with a secondary spread found in October, November, and December. The least difference of temperature, between day and night, is found in the months of May through August.

The figures for the mean minimum relative humidity vary surprisingly little with a high of 99 percent plus and lows of 96 percent in April and 94 percent in November. The mean minimum relative humidity figures mirror a plot of the number of days of no rain for each month. The high was five days with no rain in April with a secondary high of four days of no rain in November. Also revealing in the general water regime is the plot of the percentage of hours of one hundred percent humidity which shows low points in the months of April and November. The plot of direct rainfall is extremely variable from month to month but reaches peaks in the months of May, September, and December. This rainfall does not include water delivered by cloud vapor, which adds considerably to the total amount of water made available to the plants. When considering the various plots for rainfall, humidity, and temperature deviations for a single month, and in this instance the example is April, it is apparent that there is something peculiar about the composite record. Direct rainfall is high (42 cm.) yet there is a general depression of mean minimum relative humidity (78.1) and the percentage of hours of less than one hundred percent humidity (34.3), a broad spread between maximum and minimum temperature, and five days without rain. An explanation for these seemingly contradictory data can be obtained only by a close examination of the daily rainfall records — the only explanation which would account for a drop in the various humidity records and the elevation of day temperature and depression of night temperature is that the cloud cover was less than usual. There are a number of days without rain (5) and an examination of the rainfall record on a day by day basis indicates that there were several days in which rainfall was exceedingly heavy. Further, it is difficult to identify a wet season as separate from a dry season. In order to help explain the April "water" records and to identify seasonality I reinterpreted

the data by subtracting all rainfall generated by major storms. This was accomplished arbitrarily by removing all rainfall of five centimeters or more delivered in a single day. In FIGURE 6, the plot for an adjusted

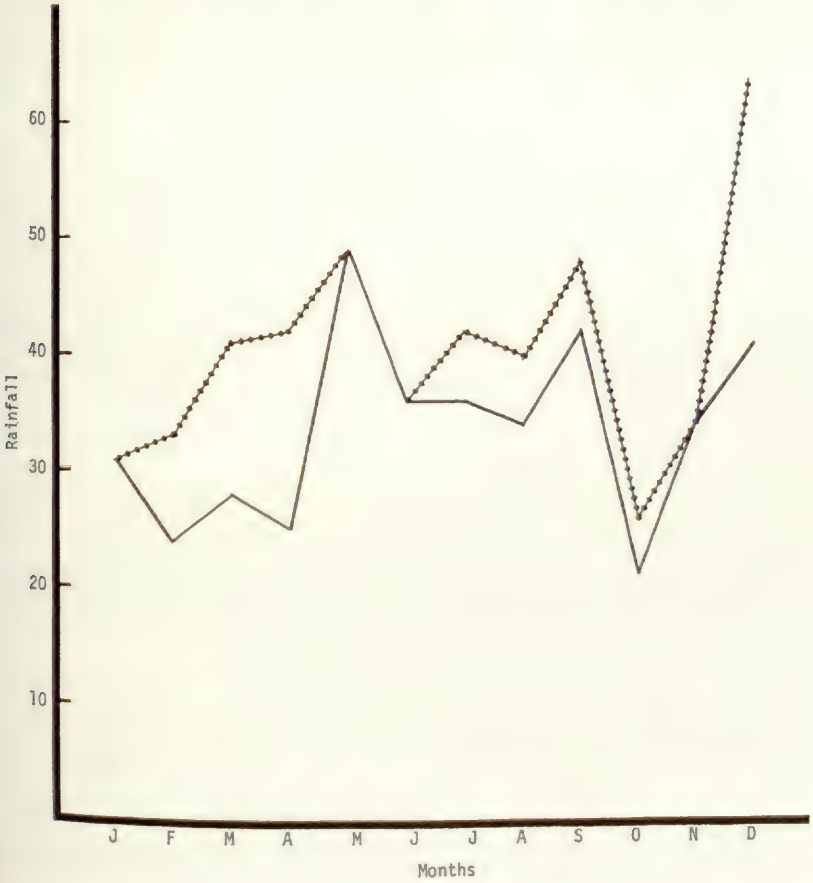

FIGURE 6. Monthly rainfall record of Pico del Oeste taken at canopy level. Solid line with diamonds = actual measurements; solid line = rainfall record adjusted by subtracting all major storms (i.e., days in which rainfall exceeded 5 cm.). This procedure helps to identify wet/dry seasonality.

rainfall record is given and the results are striking. It is possible to identify the crypto-wet/dry seasonality: the wet season being from May through September inclusive, and the time from September to May being considered the equivalent of a dry season. The wet season in Puerto Rico generally is considered to extend from April through November (see especially Odum, Drewry, and Kline, 1970). In FIGURE 7 I have extracted and replotted the rainfall data given by Odum *et al.* in their *Fig. 49c* for

El Yunque. This figure is based on data from 1958 to 1962 and corresponds fairly well with our data of 1966–67 indicating an end of the wet season in October. Janzen (1967) has noted differing lengths of the wet season in

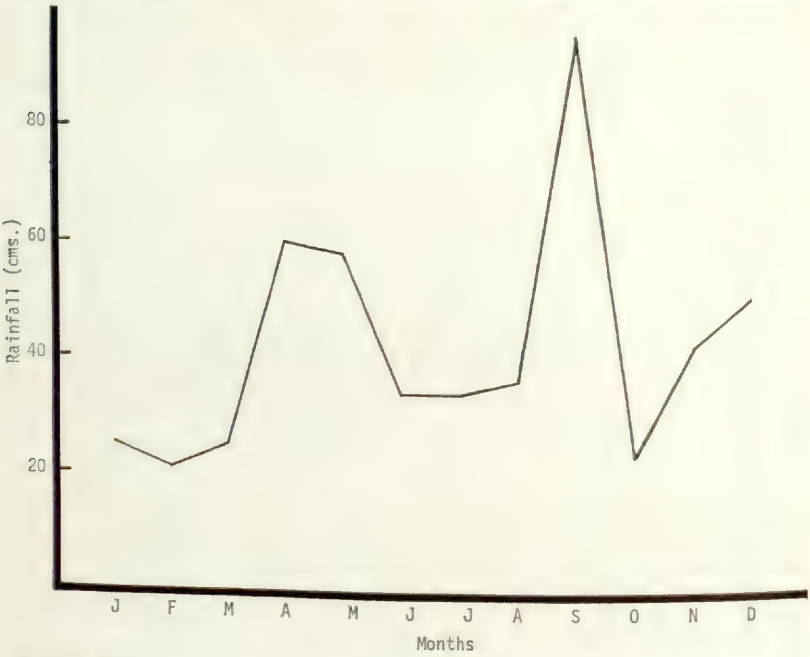

FIGURE 7. Monthly mean rainfall at El Yunque, Puerto Rico from 1958–1962. Adapted from Odum *et al.*, 1970.

Central America. On the basis of rainfall data from various parts of eastern Puerto Rico, I believe that although the total rainfall increases as altitude increases (windward side of the mountains) the length of the wet season decreases with altitude. The seasonality is masked by high total rainfall but it does exist and is an important environmental factor.

All visitors to the elfin forest, particularly those wishing to take photographs, are struck by the relatively low light intensity. Baynton (1968) suggests that over 40 percent of incident radiation is attenuated by cloud cover as the Pico seems to be enveloped by cloud for about 60 percent of the daylight hours. Spectral composition changes little with cloudiness so that available photosynthetic light also may be considered attenuated by more than 40 percent. Gates (p. 98), on the basis of energy exchange observations estimates that "it would appear that about half the maximum photosynthesis occurs for *Ocotea* and *Tabebuia*." This may account, at least in part, for the slow growth of plants on the peak (see Howard, 1969). It would seem that under such a reduced light regime competition for available light might be extremely high. There is no correlation between the total photosynthetic surface of a species and its flowering period.

Unfortunately, a full year's data on solar radiation is not available but a high of 322 Langleys per day was recorded for April. A direct correlation between amount of solar radiation and flowering periods was not established.

If we consider various environmental factors which may be important to arrive at a flowering peak in July it would appear that April might be a critical month because of its striking differences from the other months of the year. In addition to depressed rainfall, humidity, and high number of days without rain, it is on an increasing day length, the days increasing at the rate of approximately 60 seconds per day. It is possible that we are dealing with a flower bud initiation period in April so that flowering does not reach its peak until July. If true, this is a three month lag between the time of flower initiation and peak of flowering. The second highest peak of flowering occurs in October and if we assume a three month lag period between the time of flower initiation and peak of flowering, then the month of July should be significant. One is struck by the very high relative humidity, the high number of hours of one hundred percent humidity, the lack of any rain free days, and the very narrow band of temperature difference between night and day in July. In addition, day-length is decreasing at a rate of a little less than 30 seconds per day. For the July and October flowering peaks we are facing a set of contrasting environmental characteristics in April and July. April is typified by increasing day-length, depressed rainfall and humidity, increased temperature maxima, and decreased minimum temperature, while July is typified by slightly decreasing day length, high rainfall, high humidity, and little difference between day and night temperature. The question of the control of the actual flower bud initiation has not been resolved by this study although the preliminary indications point to day length control with the actual flowering modified by seasonality.

While we have stated that plants of the tropics generally respond to a marked wet/dry seasonality by their flowering cycles we have also remarked that the plants of the Pico del Oeste do not seem to do so and, in fact, many of the species have very prolonged flowering periods (see TABLE 1). FIGURE 8 is an attempt to sort out some possible flowering cycles among those species which have flowering periods less than ten months in duration, with in addition, less than one break in the flowering cycle unless that cycle is clearly bimodal. The relatively few species which fit these qualifications have been plotted in FIGURE 8. In addition, the crypto wet/dry seasonality has been indicated and an interpretation has been made on the beginning of a flowering cycle for those species in which one break in a sequence is shown. The wet season is considered to be composed of five months, May through September, during which 11 species begin their flowering. In contrast, during the seven months of the dry period only eight species begin flowering. It is the number of flowering initiations which occur in May (2), June (4), and July (4) which accounts for much of the flowering peak reached during July. If one divides the various flowering cycles as represented in FIGURE 8, according to their appearance

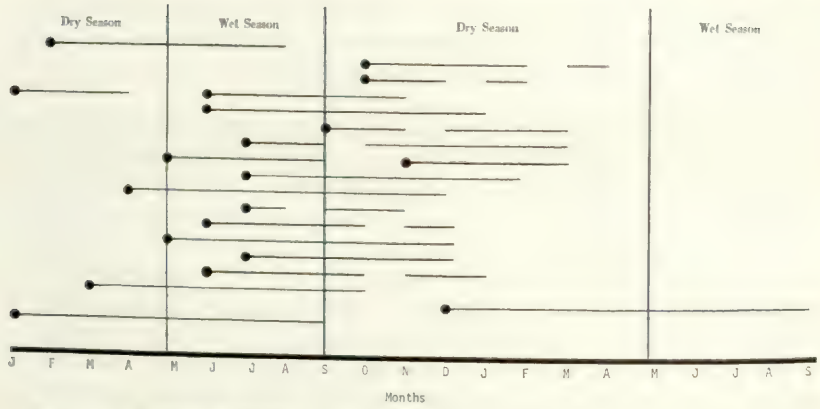

FIGURE 8. Possible flowering cycles of species with flowering periods of less than ten months and those with bimodal flowering, correlated with wet/dry seasonality. Dots indicate an interpretation of the beginning of the flowering cycle. The species included are, from top to bottom, *Mikania pachyphylla*, *Gesneria sintenisii*, *Haenianthus salicifolius*, *Micropholis garciniifolia*, *Cymbianthopsis sintenisii*, *Miconia sintenisii*, *Calycogonium squamulosum*, *Mecranium amygdalinum*, *Eugenia borinquensis*, *Calyptranthes krugii*, *Clusia grisebachiana*, *Torralbasia cuneifolia*, *Pilea krugii*, *Peperomia emarginella*, *Guzmania berteroniana*, *Carex polystachya*, *Isachne angustifolia*, *Ichnanthus pallens*.

in only one of the seasons or in a combination of seasons, the following results are obtained:

FLOWERING PERIOD	NO. OF SPECIES
During dry season only	4
Initiated in dry season, continuing into wet season	3
Initiated in dry season, continuing through wet season into next dry season	2
Initiated in wet season, continuing into dry season	11
During wet season only	0

There are two species (*Micropholis garciniifolia* and *Mecranium amygdalinum*) which have bimodal flowering, both flowering once in the dry season with the additional flowering segment initiated in the wet season and continuing into the next dry season.

It does seem that in those species of Pico del Oeste which have relatively short and more or less continuous flowering cycles that there is a marked wet dry seasonality which can be easily observed following proper interpretation of the data. Some of the flowering cycles of the Pico are very similar to those one might expect in more lowland areas of the tropics. The number of species with relatively short and stable flowering cycles is small and by rearranging the data presented in TABLE 1 according to the number of species in flower and the number of months in flower, some additional interesting aspects may be seen.

No. Months in Flower	No. of Species	% of Species in Flower in July	% of species in Flower in October
12	10	100	100
11	7	100	100
10	2	100	100
9	7	100	85
8	5	100	80
7	6	100	50
6	5	60	40
5	2	50	100
4	3	66	33
3	2	50	50
2	1	100	100
1	1	0	0
0	4	0	0

Of immediate interest is the number of species (10) and percentage of species (18%) in flower throughout the year. The number of species in flower nine or more months is 26 or 47 percent of the flora. Even more striking is the number of species (42) in flower for six or more months. In percentage this is 76 percent of the flora in flower for a prolonged period and suggests some similarity to a weed flora. It is unlike such a flora, however, because the flowering of the Pico species is rather sparse and the fruit production is low or non-existent (for a discussion of the latter situation in *Tabebuia rigida* see Nevling, 1969).

Figure 9[3] is a representation of the flowering cycle of Pico del Oeste but as a continuous record rather than as an interrupted linear sequence. In addition to presenting the yearly variation it is helpful also in visualizing the percentage of the flora in flower. The possible flowering potential for 55 species is 660 flowering months, the plants of the Pico realized approximately 64 percent of this potential. An additional 10 percent, or a total of 74 percent, is obtained if one adds the flowering records from all of Puerto Rico (see Figure 1). Thus, regardless of the method of calculating flowering time, the amount of flowering on the Pico is high.

Comparative Studies of Flowering Cycles

The limited records of flowering times of tropical plants alluded to in the opening lines of this article are no more acutely felt than when attempting to compare the flowering periodicity of one flora with that of a different area. I have not been able to locate flowering records for an additional elfin forest in the New World so that no comparison can be

[3] The graphs in this paper, with the exception of Figure 9, are presented in the traditional manner. This linear technique permits easy understanding of a year's activity but has a serious deficiency in that the January and December records are separated spatially and difficult to correlate. Figure 9 is offered as an attempt to overcome this deficiency by presenting a continuous yearly record of the percentage of the flora in flower.

made. Failing this it was hoped that a comparison of the elfin forest flora of Pico del Oeste with the adjacent rainforest flora at El Verde, Puerto Rico, could be made. Considerable effort was made to study the ecology of

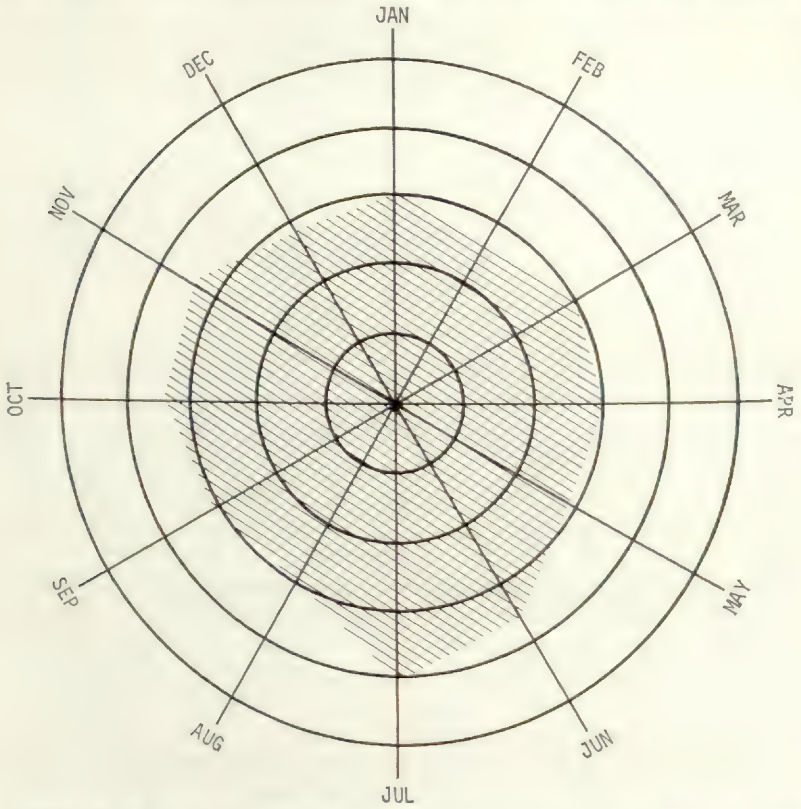

FIGURE 9. Cumulative monthly flowering record of the plants of Pico del Oeste expressed in percentage of species in flower. Each circle equals 20%.

the forest at El Verde, but unfortunately, the flowering records (Pinto, 1970; Bannister, 1970) are extraordinarily incomplete and are almost useless for comparative purposes. Therefore it was necessary to direct our comparisons elsewhere. It is possible to generate useful flowering data from local floras, particularly county floras, from temperate regions. Such a contrast of tropical flowering periods with those of temperate areas introduces a set of interesting and important questions which should be studied as data become available. Some questions are: if the floras of the world had their origins in the tropics, and assuming wet/dry seasonality existed at that time, is there any hint of how the flowering periods shifted to accommodate low temperature seasonality? Is there any relationship between tropical dry season flowering, often in a leafless condition, and the early spring flowering of temperate trees in the leafless condition? Or, is

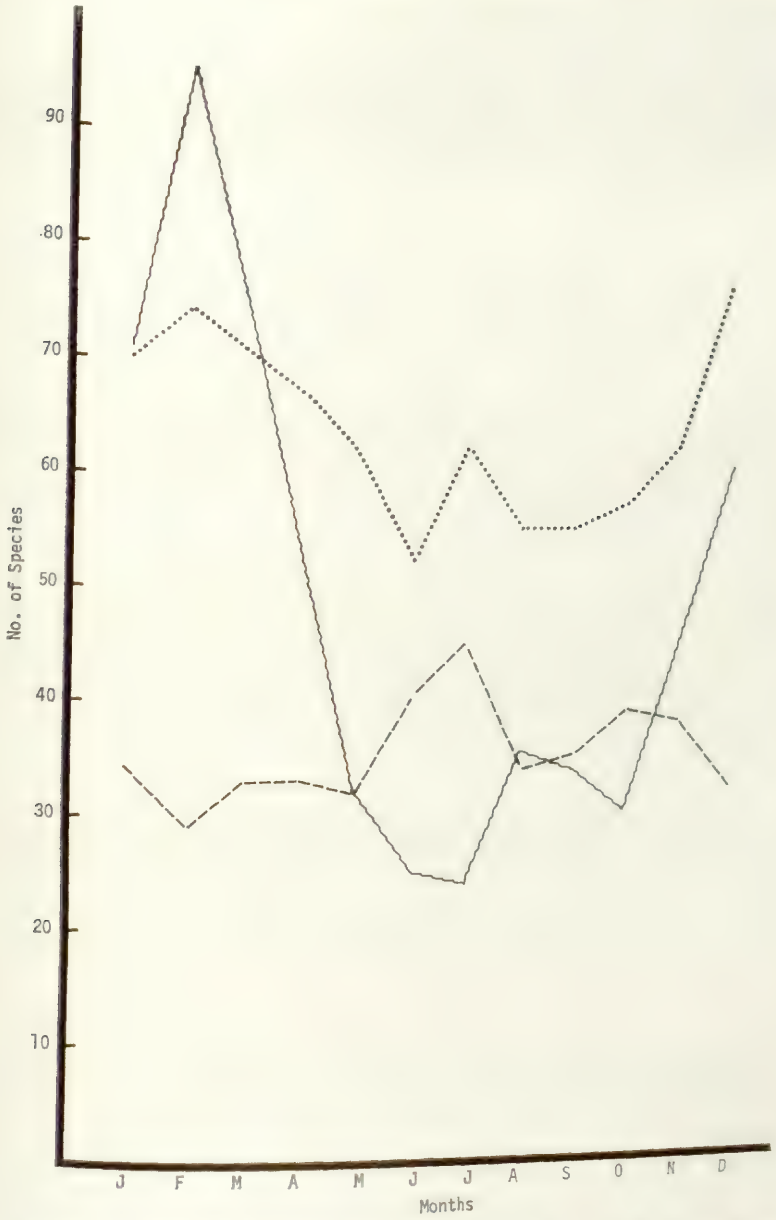

FIGURE 10. Monthly flowering records from three Neotropical areas. Wavy line = flowering of tree species from Puntarenas Prov., Costa Rica (adapted from Janzen from data by Allen). Dotted line = flowering records from Barro Colorado Island, Panama, from Croat (÷10). Dashed lines = records from Pico del Oeste, Puerto Rico.

this resemblance simply the result of a shift to wind pollination? A host of other similar questions of prime biological significance also present themselves. These questions were not explored because it seems to be an unreasonable undertaking with such limited information on tropical floras. We were able to contrast the Pico flowering with data presented by Croat (1969) for a lowland flora of Panama and to a lesser degree with data from Allen (1956) from Costa Rica. The most accessible and usable data on tropical flora with which I am familiar are those recently published by Croat for Barro Colorado Island, Panama. His flowering data were based on herbarium records and direct observations. I have manipulated his data (see Croat's FIGURE 2A) to make them compatible with the Pico data and have plotted the two together (FIGURE 10). Barro Colorado is an island about six miles square in the Canal Zone, the topographic relief is approximately four hundred and fifty feet. Croat has suggested that the forest type be referred to as semievergreen, moist tropical forest. He has recorded 1,181 species of phanerogams from the island. The climate is described as having a dry season from December to April, the rainfall then increasing gradually until a peak is reached in November. The island receives about 251 cm. of rain per year. As in the case of the Pico flora, Croat found that a surprising number of species have prolonged flowering times. His figure for species in flower for more than nine months of the year is about 41 percent or only slightly less than the 47 percent which we have reported for the Pico. In general his records when plotted with ours show similarity, although there are a few major differences. Croat's records show a major flowering peak in December, January, February, and March, which is quite dissimilar. After February, Barro Colorado flowering drops off to a low point (in June) whereas the flowering on the Pico is increasing and peaking in July. It is of interest that our July peak is mirrored by a secondary peak in Croat's records. The patterns of August and September and October are extremely similar but in Panama flowering begins to increase in November and returns to the high peak in December, while in the elfin forest the secondary peak is in October and flowering decreases in November and December. Summarizing, the two flowering records appear to be rather similar in the middle part of the year and dissimilar at the beginning and the very end of the year. Croat's major peak of December, January, February, and March is composed of both herbaceous and woody plants but after the beginning of the year the main component is the flowering of large and medium-sized trees during the dry season. His herbaceous plants peak during the months of December and January a situation quite unlike that in Puerto Rico. Flowering begins to decrease markedly in April and the composition shifts, with the flowering group composed of shrubs and small trees which have a bimodal flowering at this time, in the dry season, and again during the secondary peak of flowering in July. The July peak is composed of not only the bimodal flowering of shrubs and small trees but also of flowering of herbaceous plants. The so-called "woody vines" of Barro Colorado seem to peak and flower during the month of February and also add to the general high

flowering peak during that month. If we question the way in which the composition of the flora of Pico del Oeste differs from that of Barro Colorado Island the difference seems to be attributable to two elements: the Pico flora lacks the annual herbaceous flora, and the massive or large and medium-sized trees. The major difference existing in the flowering between the Pico and Barro Colorado occurs during the dry season and seems to be accounted for in large part by the flowering of the massive, lowland, tropical tree flora. This floristic element often flowers in the dry season in a leafless condition. There is also considerable evidence accumulating from the tropical lowlands of Central America indicating that tree-flowering is strongly correlated with the dry season (Janzen, 1967). The primary advantage of flowering during the dry season when leafless, appears to be a reduction in "internal nutrient competition" between the reproductive and the vegetative phases. If this concept is correct, one might then expect no peak flowering to occur on the Pico during the "dry season" as there are no species flowering in the leafless condition. To test this possibility further I have extracted the graphic data presented by Janzen (which he in turn extracted from Allen) for a study of tree species from Puntarenas Province, Costa Rica. These data also are shown in FIGURE 10. The data for the tree species show a very high peak of flowering in the early part of the year. The dry season in this area extends from November to April, and is followed by markedly reduced flowering from April through October, although there is a secondary peak to be found in August (homologous to our July peak?) which may possibly be caused by those species which are flowering in a bimodal condition. This is further evidence that the Pico flora flowering record is strongly affected by the lack of a major tree flora.

Some interesting flowering data also have been published by Boaler (1966) from the Lupa North Forest Reserve, Tanzania. The site is 1500 meters above sea level and has a mean annual rainfall of 90 cm. Boaler has listed the flowering species by the five seasons which he recognizes and according to their habits. His results are tabulated here for comparison.

	SEASONS				
	Dry June–Aug.	Pre-rains Sept.–Oct.	Early Rainy Nov.	Rainy Dec.–Feb.	Late Rainy Mar.–May
HABIT					
CANOPY TREES	2	6	—	—	1
UNDERWOOD TREES	3	6	—	26	18
SUFFRUTICES	—	17	23	2	4
SHRUBS	2	6	2	9	18
HERBS	1	4	4	4	5
BULBILS	—	1	5	9	2
SEDGES	—	—	9	20	21
GRASSES	—	—	9	70	69
TOTALS	8	40	52		

Once again the trees (canopy and underwood) dominate the dry season flowering. The suffrutices then assume a major flowering role from the pre-rain season through the rainy season. The herbaceous plants (including sedges and grasses) begin to come into flower in the early rainy season and peak during it. Other than the shift in calendar months for the dry and wet seasons and the relative numbers of the various habit types of data pattern seems not unlike that given for Pico del Oeste. It is curious to note again that grasses and sedges, presumably wind pollinated, peak during the rainy season when apparently at a serious disadvantage. I believe that the comparative studies furnish evidence that the flowering pattern exhibited by the plants of Pico del Oeste is not basically different from that which one finds under other tropical conditions but the differences which appear are primarily the result of the absence of massive and medium-sized trees which typify the lowland rain forest.

FRUITING

It has been reported in several of the preceding papers of this series that considerable vegetative reproduction is to be found on the Pico. The environmental characteristics of the site are similar to those reproduced

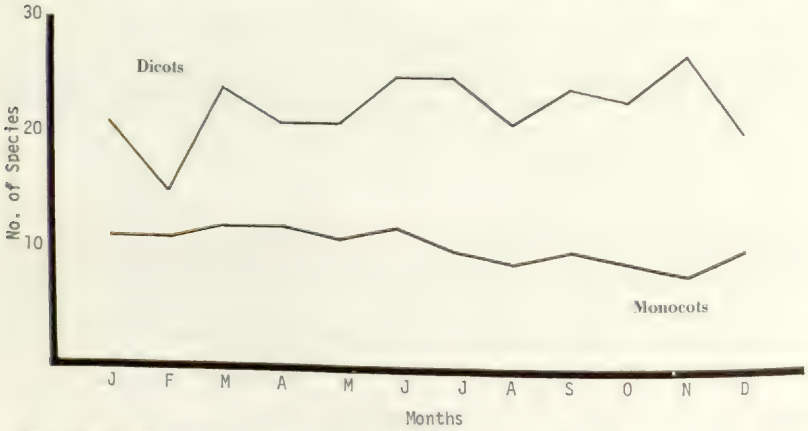

FIGURE 11. Cumulative monthly fruiting records of the species of Pico del Oeste.

in mist tents so widely employed by plant propagators today. It is not surprising that almost every broken branch develops a root system and has the possibility of becoming established as an individual plant. In actual total reproduction, asexual reproduction has clearly outstripped sexual reproduction during the course of this study. For example, it is possible that one of the major tree species, *Tabebuia rigida*, is represented by only one or a few clones which have, through vegetative reproduction, come almost to dominate the area. Extensive root grafting among individuals of the same and of different species is so prevalent that it is no longer

possible to isolate distinct trees. The effect of the peculiar environment of the Pico has been to permit or even to promote the amount of vegetative reproduction.

The records for fruiting (FIGURE 11) are more uneven than those for flowering, for a variety of reasons but mostly involving the observation team. There was a general tendency to score a species in fruit as soon as fruit-set was observable and perhaps FIGURE 11 is a better record of that phenomenon than of fruiting. Fruiting implies that some fruits mature but in fact, very few species did carry fruit to maturation. The initial fruit-set was low, perhaps due to the paucity of pollinators, a lack of proper environmental factors or both. In those cases where fruit-set occurred the young fruits were subject to bird and insect predation to the degree that very few species brought fruit to maturation. In this context the existing environmental characteristics of the site must be considered as extremely harsh. Only *Eugenia borinquensis*, *Symplocos micrantha*, and *Vriesea sintenisii* seemed to fruit on a regular basis and produce seedlings which were observed.

We are faced with the fact that the flora on Pico del Oeste is not reproducing sexually on a regular cyclic basis. The additional fact that such a large percentage of species have prolonged flowering periods may indicate an adaptation permitting sexual reproduction whenever the proper conditions occur, regardless of season. Such proper conditions may not have occurred during the more than two years of our observations. If this conclusion is correct, it may be that the sexual reproductive cycle is effective only once in a variable number of years and accounts for the lack of annuals in the flora. Only species which have a long generation pattern can reproduce sexually in the ecologically specialized habitat of the elfin forest. The consequence of intermittent and irregular sexual reproduction is a general slowing of evolutionary processes leading to poor species diversity. This seems to be the case as the 55 species of the flora are distributed in 50 genera with more than one species occurring only in *Peperomia* (2), *Pilea* (2), *Miconia* (3), and *Psychotria* (2). The elfin forest is not an area where active speciation is occurring: if it were, endemic species would have developed. A second possibility is that, with few exceptions, the elfin forest flora never reproduces sexually and the area is continually or occasionally supplied with new propagules from individual plants growing at somewhat lower altitudes. On a regular basis the propagules could be brought to the peak by birds and in other cases the fruits could be carried by high winds associated with travelling storms. That this has happened is proven by the few individuals of *Hillia parasitica* and *Trichilia pallida* found on the site. Whether there is rare effective sexual reproduction *in situ* or a continuing supply of propagules from lower altitudes, the role of vegetative reproduction is the predominant force in maintaining the floristic composition of the peak once it is established.

In summary, it seems to me, on the basis of the flowering and reproductive patterns shown by the plants of Pico del Oeste, that the flora is similar

to a tropical flora from lower altitudes minus some elements. The flora of the Pico has been derived from only a portion of such a flora. The missing elements are the herbaceous annuals and the massive and medium-sized trees. A firm indication of wet/dry seasonality remains in spite of the high total rainfall of the area. The effective species filter of the annuals and large trees is to be found in the total climatic conditions present but most especially in the low light intensity. The Pico del Oeste flora seems to be an aggregation of species with a common ability to survive under a low light regime and one which had its origin in the rainforest.

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TAXONOMIC AND NOMENCLATURAL NOTES ON JAMAICAN GAMOPETALOUS PLANTS

WILLIAM T. STEARN

PREPARATION OF A *Flora* of a tropical area almost invariably reveals a need for alteration of existing classifications of genera and species, for changes in nomenclature, and for establishment of new taxa by publication of Latin diagnoses or descriptions. These usually require more extended explanation than befits the concise formal style of the *Flora* itself and are best published elsewhere. Thus from 1912 onwards William Fawcett (1851–1926), Spencer LeMarchant Moore (1850–1931) and Alfred Barton Rendle (1865–1938) published in the *Journal of Botany, British and Foreign* a series of notes on such matters concerning Jamaican plants to serve as precursors to volumes 3 to 7 of the *Flora of Jamaica*. The following notes deal with some problems of nomenclature and taxonomy relating to *Alectra* (Scrophulariaceae); *Bourreria* and *Cordia* (Boraginaceae); *Forestiera* (Oleaceae); *Justicia*, *Oplonia*, and *Ruellia* (Acanthaceae); *Solanum* (Solanaceae); *Tabernaemontana* (Apocynaceae); and *Tournefortia* (Boraginaceae) which have become evident when working upon volume 6 of the *Flora of Jamaica*.

OLEACEAE

Forestiera rhamnifolia Griseb. Cat. Pl. Cuba 169. 1866.
Var. **rhamnifolia**.

Grisebach based his *Forestiera rhamnifolia* on glabrous specimens gathered in western Cuba by Friedrich Rugel (1806–1879) and Charles Wright (1811–1885), as is evident from his protologue: "8. FORESTIERA RHAMNIFOLIA Gr. in pl. Rugel. glabra, foliis (2″ longis) rigidis ellipticis integerrimis v. saepius superne serrulatis subtus punctatis petiolatis, drupa ellipsoidea (4″ longa) utrinque acutiuscula pedicello longiori. — Cuba occ., in rupibus supra Punta brava (Rug. 792; Wr. 2939) E. [= Endemica]."

Since *Wright 2939* in Grisebach's herbarium at the Systematisch-Geobotanisches Institut der Universitat Göttingen (GOET) is from "La Termine," whereas *Rugel 792* is labeled "Ad rupes supra Punta brava, ins. Cuba," a locality about fifteen miles west of Habana, Rugel's material should be taken as lectotype. The leaves of all these specimens are quite glabrous, as they are in *Ekman 13377* and *Wilson 9176* from La Habana province, and in *Ekman 13042* and *Britton & Earle 7639* from Pinar del Rio province in western Cuba. In all specimens seen from Jamaica, the leaves are pilose beneath with spreading hairs, particularly noticeable

along the midrib and main veins. The leaves of a specimen from Oriente province (*Ekman 15580*) are also hairy beneath though less profusely so than in Jamaican material. These pilose specimens represent a geographical race worthy of note.

Var. **pilosa** Stearn, var. nov. PLATE I.

Folia subtus pilis brevibus vix 0.4 mm. longis numerosis vestita.

Jamaica. ST. ELIZABETH: Santa Cruz Mounts, 1842, *Purdie* (K). ST. ANDREW & KINGSTON: Gordon Town Road, iv. 1905, *Harris 8938* (BM; K), *Harris 8526* (BM). Road to Wareka, Long Mountain, x. 1905, *Harris 9017* (BM, holotype; K). Long Mountain, north side, xi. 1905, *Harris 9056* (BM; K). PORTLAND: Hall's Delight, 1500 ft. ix. 1897, *Harris 6818* (BM). ST. THOMAS: above Windsor Forest fording, 1200 ft. 12 vi. 1960, *Adams 7260* (BM). **Cuba:** ORIENTE: Victoria de las Tunas, Finca Potosi, x. 1922, *Ekman 15580* (BM).

APOCYNACEAE

TABERNAEMONTANA IN JAMAICA

The Jamaican species of *Tabernaemontana* were independently and perhaps simultaneously revised, shortly before 1938, by Friedrich Markgraf in Berlin, R. E. Woodson in St. Louis, and A. B. Rendle in London. Markgraf's synopsis formed part (pp. 168–171) of a survey of "Die amerikanischen Tabernaemontanoideen" published in *Notizbl. Bot. Gart. Berlin* **14**: 151–184 "ausgegeben am 10 Juli 1938"; he provided a key, synonymy and citations of specimens but no descriptions. Woodson's work formed part (pp. 105–111) of his account of the family Apocynaceae in the *North American Flora* 29 no. 2 "published . . . July 11, 1938"; he provided a key, synonymy and detailed descriptions but no citations of specimens. Rendle, who died on 11 January 1938, had written in 1937 an account of the Jamaican species as text for volume 6 of Fawcett & Rendle's *Flora of Jamaica*, which neither he nor Fawcett lived to complete, and I found the manuscript among Rendle's unpublished notes when I resumed work on the *Flora*. These three accounts do not completely tally, and correlation indeed proved a little difficult because their authors worked with a slightly different and limited range of material and presented their results in different styles. The specimens then available had been collected by Sloane, Swartz, Wiles, Wullschlägel, Purdie, Alexander, Harris, and Britton, but in no one institution were all gatherings represented. Because of these discrepancies and since I had available the types or isotypes of all the described Jamaican species as well as extensive recent collections made by Proctor, Adams, and myself, I prepared yet a fourth independent account and later correlated it with the others. Since the alkaloids of these plants have a pharmacological interest, the following summary of the result is presented as a concise guide; it comes from a more detailed

account prepared for the *Flora of Jamaica*. Two species of the related group *Ervatamia* are cultivated in Jamaica, *E. divaricata* (L.) Burkill (*Tabernaemontana coronaria* Willd.) in its double-flowered form and *E. pandacqui* (Poiret) Pichon (*Tabernaemontana cumingiana* A. DC.), and also one species of *Voacanga*.

All Jamaican species of *Tabernaemontana* appear to be endemic and they have distinctive ranges (see FIGURE 1 A and B). Sir Hans Sloane collected in 1688 or 1689 the lowland, usually coastal, species which Linnaeus in 1753 named *Tabernaemontana laurifolia*. Linnaeus had no material of this but knew it through Sloane's description and illustration in his *Voyage to . . . Jamaica* 2: 62. *t. 186, f. 2*. 1714; accordingly the specimen in Herb. Sloane 6 fol. 58 (BM) on which these are based can be accepted as the typotype of *T. laurifolia*.

In 1788 Swartz published *Tabernaemontana discolor*, unfortunately without giving any precise locality. It has been collected since only once, by Wiles (K), who also gave no locality. Woodson, who never saw true *T. discolor*, equated it with *T. ochroleuca*, described by Urban in 1909, and known only from Dolphin Head in Hanover Parish. *T. wullschlaegelii* described by Grisebach in 1861 from specimens collected by Wullschlägel, no. *918* (GOET, M), on the other hand, has been collected several times since and is evidently fairly widespread in the upland wooded region of central Jamaica. The related *T. rendlei* is geographically remote from this locality, being confined to the John Crow Mountains in the east.

1. Corolla tube 14–18 mm. long.
   2. Leaf blades mostly more than 10 cm. long, with 7 to 11 nerves each side of the midrib and an evident network of veins between them. Corolla swollen at insertion of stamens on upper 1/4 of tube. Coastal. . . . . 1. *T. laurifolia*.
   2. Leaf blades less than 10 cm. long, with 4 to 6 nerves each side of the midrib and other veining faint. Corolla swollen at insertion of stamens on middle of tube. . . . . 2. *T. discolor*.
1. Corolla tube 5 to 11 mm. long.
   3. Leaf blades small, less than 8 cm. long, with 5 to 7 nerves each side of the midrib. Calyx 1.5–2 mm. long, the sepals acute. Corolla swollen at insertion of stamens on upper 1/3 of tube. . . . . 3. *T. ochroleuca*.
   3. Leaf blades larger, up to 20 cm. long, with usually more than 7 nerves each side of the midrib. Calyx 2–3 mm. long, the sepals obtuse or rounded. Corolla swollen at insertion of stamens on middle of tube.
      4. Corolla lobes about 14 mm. long. . . . . 4. *T. ovalifolia*.
      4. Corolla lobes about 5–7 mm. long.
         5. Corolla with tube about 5–6 mm. long, lobes 4–5 mm. long. Follicles (mericarps) semiorbicular. Central Jamaica. . . . . 5. *T. wullschlaegelii*.
         5. Corolla with tube about 7–8 mm. long, lobes 7 mm. long.
            6. Leaves glaucescent. Follicles almost lanceolate in outline. Northwestern Jamaica. . . . . 6. *T. glaucescens*.
            6. Leaves yellowish green. Follicles unknown. John Crow Mountains, eastern Jamaica. . . . . 7. *T. rendlei*.

1. **T. laurifolia** L. Sp. Pl. 1: 210. 1753; Markgraf, Notizbl. Bot. Gart. Berlin 14: 169. 1938; Woodson, N. Am. Fl. 29: 109. 1938.

Nerium arboreum, folio latiore obtuso, flore luteo minore Sloane, Cat. Pl. Jam. 154. 1696; Voy. Jam. 2: 62. *t. 186. f. 2.* 1714.

This Jamaican species inhabits coastal woodland and thickets at 10 to 60 feet (3–18 m.). It has been collected in the parishes of HANOVER (*Proctor 11256*); WESTMORELAND (*Proctor 11108, 11122*; *Adams 10957*; *Webster 8506*; *Stearn 393*); ST. ELIZABETH (*Harris 9933*; *Stearn 887*); MANCHESTER (*Stearn 645*); ST. ANN (*Stearn 316; Stearn 728*); ST. CATHERINE (*Sloane*); ST. MARY (*Stearn 779*; *Prior*); ST. ANDREW (*Harris 10388*) and ST. THOMAS (*Purdie*; *Stearn 692*; *Proctor 15567*).

2. **T. discolor** Swartz, Prodr. 52. 1788; Fl. Ind. Occ. 1: 535. 1797; Urban, Symb. Antill. 5: 463. 1908, 7: 333. 1912; Markgraf, Notizbl. Bot. Gart. Berlin 14: 168. 1938.

A little known but well-marked Jamaican species, known only from unlocalized collections by Swartz made "in Jamaicae frutetis" and by Wiles. Woodson's account of "*T. discolor*" was based on specimens of *Tabernaemontana ochroleuca*.

3. **T. ochroleuca** Urban, Symb. Antill. 6: 34. 1909; Markgraf, Notizbl. Bot. Gart. Berlin 14: 168. 1938.

T. discolor sensu Woodson, N. Am. Fl. 29: 109. 1938.

A species known only from gatherings made on Dolphin Head, HANOVER PARISH (*Purdie*; *Harris 10297*, type-collection; *Webster & Wilson 5081*). at 1000–1700 ft. (300–500 m.).

4. **T. ovalifolia** Urban, Symb. Antill. 5: 462. 1908; Markgraf, Notizbl. Bot. Gart. Berlin 14: 169. 1938; Woodson, N. Am. Fl. 29: 107. 1938.

This species is also known only from Dolphin Head, HANOVER (e.g. *Harris 9239, 10276*) at 900–1200 ft. (270–360 m.).

5. **T. wullschlaegelii** Griseb. Fl. Brit. W. Ind. Isl. 409. 1861; Markgraf, Notizbl. Bot. Gart. Berlin 14: 169. 1938; Woodson, N. Am. Fl. 29: 107. 1938, excluding as a synonym *T. glaucescens*.

T. lactea Urban, Symb. Antill. 6: 34. 1909.
T. calcicola Urban, Repert. Sp. Nov. 13: 472. 1915.

T. wullschlaegelii is an inland and upland species which has been collected at 1400–3000 ft. (420–910 m.) in the parishes of TRELAWNY (*Harris 8815*, type-collection of *T. lactea*; *Proctor & Alain 24906*); MANCHESTER (*Harris 8412*; *Harris 8267*; *Wullschlägel 918*, type-collection of *T. wullschlaegelii*; *Purdie*; *Adams 12491*; *Adams 10123*); CLARENDON (*Harris 11045*, type-collection of *T. calcicola*); ST. ANN (*Alexander*;

Proctor & Skelding 16137; *Britton & Hollick 2809*; *Proctor 23439*), and ST. CATHERINE (*Howard & Proctor 15079*).

6. **T. glaucescens** Urban, Symb. Antill. 6: 35. 1909; Markgraf, Notizbl. Bot. Gart. Berlin 14: 168. 1938.

A little known, apparently coastal or lowland species collected by Harris (no. *10358*) at Roaring River, near St. Ann's Bay, ST. ANN and also at Fray Woods, HANOVER, this was united by Woodson with the inland *T. wullschlaegelii* from which it differs by its narrow elongated carpels.

7. **T. rendlei** Stearn, sp. nov.

Frutex vel arbor parva, glabra, 5.5–8 m. alta. *Ramuli* annotini et vetustiores pallide grisei, longitudinaliter sulcati. *Folia* chartacea in eodem pari inaequalia; lamina plerumque oblongo-elliptica, interdum anguste lanceolata, apice breviter abrupteque acuminata, basi cuneata parum attenuata, 4.5–20 cm. longa, 2–8 cm. lata, flavido-viridia, nerviis utroque latere costae 9–12 sug angulo 70°–80° abeuntibus. *Inflorescentia* subcorymbosa, multiflora, laxa, iterum et iterum ramosa, ca. 2–4 cm. longa, subsessilis vel breviter pedunculata; bracteolae ca. 0.6 mm. longae; pedicelli graciles, 5–10 mm. longi; alabastri obtusi. *Calyx* ca. 2–2.5 mm. longus, viridis, segmentis imbricatis rotundatis. *Corolla* hypocrateriformis, fragrans; tubus ca. 7–8 mm. longus, viridulus, medio ca. 1.5–1.8 mm. crassus et parum dilatatus; segmenta patula, ca. 6–8 mm. longi, 3 mm. lati, albi, margine revoluta. *Stamina* ca. 4 mm. supra basim corollae inserta; antherae ca. 3 mm. longae, viridi-marginatae.

Jamaica. PORTLAND: Northwest slope of Joe Hill, 1000–2250 ft. in moist secondary rain-forest, iv. 1956, *Proctor 10112* (BM; IJ). East slope of John Crow Mountains 1 1/2–2 miles southwest of Ecclesdown, iv. 1955, *Proctor 9982* (IJ). Three miles southwest of Priestman's River, 1200 ft. ii. 1953, *Proctor 7643* (IJ). ST. THOMAS: East slope of south end of John Crow Mountains, 11 iii. 1909 *Harris & Britton 10728* (BM, fragment; K, NY). Big Level district, southwest end of John Crow Mountains, 1500–2000 ft., 16 iii. 1956, *Stearn 509* (BM, holotype; A).

Apparently an endemic species of the moist John Crow Mountains of eastern Jamaica. *Tabernaemontana rendlei* grows between 300 and 670 meters. Albert Barton Rendle (1865–1938), who from 1906 to 1930 was keeper of the Department of Botany, British Museum (Natural History), recognized it as a new species when preparing an account of the Apocynaceae of Jamaica, and it has accordingly been named in his memory. Proctor and I found it in full flower at the south end of the John Crow Mountains in March, 1956, but unfortunately did not see any fruits. The cited information above as to the color of the leaves, corolla, and anthers was noted then in the field. Using Woodson's key (N. Am. Fl. 29: 105, 106. 1938), and also Markgraf's (Notizbl. Bot. Gart. Berlin 14: 132. 1938), this goes down to *T. wullschlaegelii*, a species of central Jamaica with smaller flowers.

BORAGINACEAE

Bourreria

About 1732, towards the end of his stay in Regensburg, the German botanical artist Georg Dionys Ehret (1708–1770), then young and virtually unknown, became friendly with a young pharmacist training in Nürnberg, Johann Ambrosius Beurer (1716–1754), who recognized his talent and put him in touch with the celebrated doctor, bibliophile, and botanist Johann Christoph Trew (1695–1769) of Nürnberg. Beurer subsequently became owner of the Spitalapotheke in Nürnberg and a member in 1750 of the Academia Caesarea Leopoldino-Carolina Naturae Curiosorum, and was reputed a good botanist. Years later, in memory of their friendship, Ehret, now celebrated and settled in England, published a plate with diagnostic details of a new genus in his *Plantae et Papiliones Rariores t. 13.* 1755, which he named *Beureria*. As regards the name he stated that "Nomen gerit Celeb. Joh. Ambrosii BEVRER, Pharmacopaei xenodochialis Norimbergensis," Beurer being pharmacist to the Fremdenhospital zum Heiligen Geiste in Nürnberg, and "Hos BEVERIAE characteres primas observavi, descripsi atque delineavi Ao 1749." The plant depicted is *Calycanthus floridus* L. (1759) and the generic name *Calycanthus* L. (1759) has had accordingly to be conserved against *Beureria* Ehret (1755).

Ehret drew and engraved the plates for Patrick Browne's *Civil and Natural History of Jamaica* (1756) and doubtless he told Browne about his old friend Beurer. Browne seemingly misheard Ehret and in his *Civil and Natural History of Jamaica* 168. *t. 5, f. 2.* 1756, he founded a genus *Bourreria*. "I have named it," he said, "after Mr. Bourer, an apothecary of Nüremberg, who was a great promoter of natural history." This erroneous spelling *Bourreria* was corrected to *Beureria* in Browne's index (p. 492). Jacquin, having adopted *Bourreria* in 1760 (Enum. Syst. Pl. Carib. 2. 14) emended this to *Beurreria* in 1763 (Select. Stirp. Amer. 44). C. F. Gaertner (Suppl. Carpol. 170. 1807) accepted this compromise spelling *Beurreria* as did Kunth (Nova Genera 3: 66. 1818) and George Don the Younger (Gen. Syst. Garden. Bot. 4: 389. 1838). The correct spelling *Beureria* was used by Sprengel (Syst. Veg. 1: 647. 1824), Grisebach (Fl. Brit. W. Ind. Isl. 481. 1862), Gürke (in Engler & Prantl, Pflanzenfam. IV. 3a: 86. 1893) and O. E. Schulz (in Urban, Symb. Antill. 7: 45–71. 1911). Schulz's work is the last revision of the whole genus. Nevertheless, despite this consensus of learned usage, in favor of *Beur-* against *Bour-*, Browne's erroneous first spelling *Bourreria* was officially conserved after the Sixth International Botanical Congress at Amsterdam in 1935 (cf. Kew Bull. 1940: 121), probably by oversight, as stated by Rickett and Stafleu (Taxon 8: 83. 1960), and so we are stuck with it.

Browne based his *Bourreria* on a Jamaican plant, well illustrated by Ehret, with which Linnaeus became acquainted at first hand when he bought Browne's herbarium in 1758. Linnaeus did not accept Browne's genus but fused it with *Cordia* and named the species *Cordia Bourreria*

(in his Systema Naturae ed. 10. 2: 736. 1759). His entry under genus 228, *Cordia*, runs:

> *Bourreria* 3. C. fol ovatis integerrimis, fl.
> subcorymbosis, calyce-laevibus. *Brown.*
> *jam.* 168. *t.* 15. f. 2. *Plum ic.* 105
> *Comm. amst.* 1. *t.* 79.

There are three elements in this: 1) a plant from Jamaica figured by Browne; 2) a plant figured by Plumier which is *Cordia sebestana* L. and must have been included by accident; 3) a plant from Curaçao figured by Commelin, *Rar. Pl. Horti. Med. Amstelod.* 1: 153. *t. 79.* 1697, as *Mespilus Americana lauri-folia glabra*. The lectotype of *Cordia bourreria* must obviously be Browne's Jamaican plant, represented by Linnaean Herb. 254.2.

This Linnaean specimen from Browne has closely appressed minute gray hairs covering the inflorescence and the calyx and also the underside of the leaf; it represents a species common in Jamaica which Miers described in 1869 under *Crematomia molliuscula* and other names. Linnaeus in 1762 (Sp. Pl. ed. 2. 1: 275) transferred this from *Cordia* to *Ehretia* as *E. Bourreria*.

In 1838, in his *Sylva Telluriana Mantissa Synoptica*, Rafinesque published a nomenclaturally important note on *Bourreria* as follows: "203. BOURRERIA Br. Jaq. Ad. Kunth, &c, dif. Ehretia, cor. hypocrat. tubo elong. limbo plano lac. dilatatis vel obcord. drupis 4gonis, 4sulcat. nucibus 2 utrinque 2 sp. *fl.* corymbosis. To this belong *B. baccata* (E. Bour. L.) and *B. exsuca* Jaq. Perhaps some others, more like some Cordias than Ehretias." Rafinesque's new name *B. baccata*, being based on *Ehretia bourreria* (L.) L., necessarily has the same type, i.e. *Cordia bourreria* L., and is thus the earliest specific name available for the Jamaican *Bourreria* with appressed pubescence. This species is accordingly the type species of *Bourreria* P. Browne.

Familiar with *Cordia*, *Bourreria*, and *Ehretia* in a living state which he saw while in the Caribbean region from 1755–1759, Jacquin accepted the genus *Bourreria* in 1760 (Enum. Syst. Pl. Carib. 2, 14), but provided a generic diagnosis of his own, "*Bacca* 4-sperma. *Sem.* 2-locularia. *Cor.* hypocrateriformis," and also diagnoses of two new species:

> *succulenta* 1. BOURRERIA fructibus succulentis.
> *Comm. Amst. t.* 79.
> *exsucca* 2. ——— fructibus exsuccis.

In 1763 (Select Stirp. Amer. 44) under the emended name *Beurreria*, Jacquin gave detailed descriptions based on living material examined in Martinique and Curaçao for *B. succulenta* and at Cartagena, Colombia, for *B. exsucca*. Neither name was based on Jamaican material, although Jacquin in 1763, but not in 1760, cited synonyms of Browne and Sloane referring to Jamaican plants. Since Jacquin figured a specimen from

Martinique, in his *Observ. Bot. t. 26.* 1767, as representing his *B. succulenta*, Martinique can be accepted as its restricted type locality.

In 1869 John Miers, at the age of 79, published a survey of *Bourreria* which he divided into two genera, i.e. *Bourreria* proper and *Crematomia*, typified by *B. exsucca*. This appeared in *Ann. Mag. Nat. Hist.* IV. 3: 199–210, 300–313. [Mar.-Apr.] 1869, and was reprinted in his *Contributions to Botany* 2: 230–242. He was an acute and accurate observer, who retained into old age an intense curiosity about morphological details which he investigated with assiduity, and as a retired chemist and engineer, he brought to his botanical studies the precision of his former callings, together with a somewhat mechanical approach. As William Carruthers remarked in his obituary of Miers (Jour. Bot. (London) 18: 36. 1880), "he had a very quick sense of differences, but he sometimes failed to distinguish the real value of the differences he saw." The editor, M. T. Masters, of the *Gardeners Chronicle* (cf. 1879. 2: 522. [Oct.] 1879) said much the same: "as a botanist his tendency was to minute elaboration rather than judicial estimate of the relative importance of details. In practice, therefore, he multiplied species, and even genera and orders, to an extent opposed to the prevailing tendencies of his contemporaries. Miers never adopted the doctrine of the mutability of the species"; he was 70 when Darwin published *The Origin of Species*. Seemingly he took as representing a well-marked species any herbarium specimen or little group of herbarium specimens which differed in appearance from other specimens. Thus, on the evidence of sixteen specimens in the British Museum and Kew herbaria, he recorded nine taxa from Jamaica under the names *Bourreria succulenta*, *B. ovata*, *B. rigida*, *B. tomentosa*, *Crematomia venosa*, *C. attenuata*, *C. elongata*, *C. molliuscula*, *C. velutina*, these being described accurately but defined vaguely. O. E. Schulz in 1911 reduced them all to three, *B. succulenta*, *B. velutina*, and *B. velutina* var. *venosa*. The variability within populations in the genus, particularly as regards leaf shape, is so great that only a few inconspicuous inflorescence and floral characters seem constant enough over large areas to serve for the distinction of taxa. Thus the character separating *B. succulenta* from its allies is its undivided style, to which Schulz attached much importance and which certainly seems unvarying in the material available over most of the West Indies. In Jamaica, however, there are rather similar plants but with the style deeply divided. For these the name *B. venosa* is used here, although with some doubt as to the importance of the distinction. Four Jamaican taxa, closely allied, may be distinguished as follows:

1. Inflorescence and outside of calyx covered completely with short whitish hairs visible under a lens.
   2. Hairs of inflorescence and calyx appressed. Widespread. ..... 1. *B. baccata.*
   2. Hairs of calyx erect or spreading. St. Catherine. ..... 2. *B. velutina.*
1. Inflorescence and outside of calyx glabrous or, rarely, with a few scattered hairs.
   3. Style divided into two branches 1–2.5 mm. long, hence with two stigmas each about 1 mm. broad. Widespread. ..... 3. *B. venosa.*

3. Style not divided but grooved at apex, hence with one bilobed stigma 1–2 mm. broad. St. Andrew. ..... 4. *B. succulenta.*

1. **Bourreria baccata** Raf., Sylva Tellur. 42. 1838. FIGURES 1E; 2A.

Bourreria arborea foliis ovatis alternis P. Browne, Civil & Nat. Hist. Jam. 168. *t. 15. f. 2.* 1756.

Cordia bourreria L. Syst. Nat. ed. 10. **2:** 936. 1759, sensu stricto.

Ehretia bourreria (L.) L. Sp. Pl. ed. 2. **1:** 275. 1762.

Bourreria rigida Miers, Ann. Mag. Nat. Hist. IV. **3:** 204. 1869; Miers, Contrib. Bot. **2:** 236. 1869.

Crematomia elongata Miers, tom. cit. 308. 1869; Miers, Contrib. Bot. **2:** 250. 1869.

Crematomia molliuscula Miers, tom. cit. 309. 1869; Miers, Contrib. Bot. **2:** 252. 1869.

Beureria velutina sensu O. E. Schulz in Urban, Symb. Antill. **7:** 62. 1911, maj., non (DC.) Gürke.

Evidently widespread in Jamaica, where it ranges from sea-level to 3000 ft. (900 m.), this has been collected in the parishes of ST. JAMES (*Stearn 615*); TRELAWNY (*West & Arnold 782*); MANCHESTER (*Howard & Proctor 14328*); CLARENDON (*Proctor 10219*; *Proctor 8215*; *Lewis 2851*); ST. ANN (*Alexander 564*); ST. CATHERINE (*Harris 6763*); ST. ANDREW and KINGSTON (*McNab*; *Campbell 5774, 6151*; *Harris 11774*; *Webster 4996*; *Yuncker 17066, 18149*).

I have taken as the lectotype of *Bourreria baccata* Raf. a specimen from *P. Browne* in the Linnaean Herbarium 254.2 (LINN), of *B. rigida* Miers one from *Houstoun* (BM), of *Crematomia elongata* Miers one from *Bancroft* (K, BM; drawing of K specimen by Miers), of *C. molliuscula* Miers one from McNab collected near Halfway Tree (K, BM; drawing of K specimen by Miers).

2. **Bourreria velutina** (DC.) Gürke in Engler & Prantl, Pflanzenfam. IV. **3a:** 1893, as "Beureria"; O. E. Schulz in Urban, Symb. Antill. **7:** 62. 1911, pro parte min. FIGURES 1E; 2B.

Ehretia velutina DC. Prodr. **9:** 508. 1845.

Crematomia velutina (DC.) Miers, Ann. Mag. Nat. Hist. IV. **3:** 310. 1869; Miers, Contrib. Bot. **2:** 252. 1869.

Small tree or shrub to 4 m. high; younger branchlets puberulous with soft whitish erect or ascending hairs to 0.5 mm. long, older ones glabrous and gray. *Leaves* scattered or crowded, variable in shape and size on the same plant; blade oblong-elliptic, broadly elliptic, oblanceolate or obovate, with the apex usually rounded or obtuse, rarely subacute, margin entire, base narrowly or broadly cuneate, 2–9 cm. long, 1.5–4 cm. broad, with 6–8 pale curved nerves each side of the midrib connected by a fine slightly raised network of veinlets, strigulose above with short almost appressed hairs, puberulous below with short soft ascending hairs especially along the midrib and nerves, chartaceous; petiole 3–9 mm. long, puberulent.

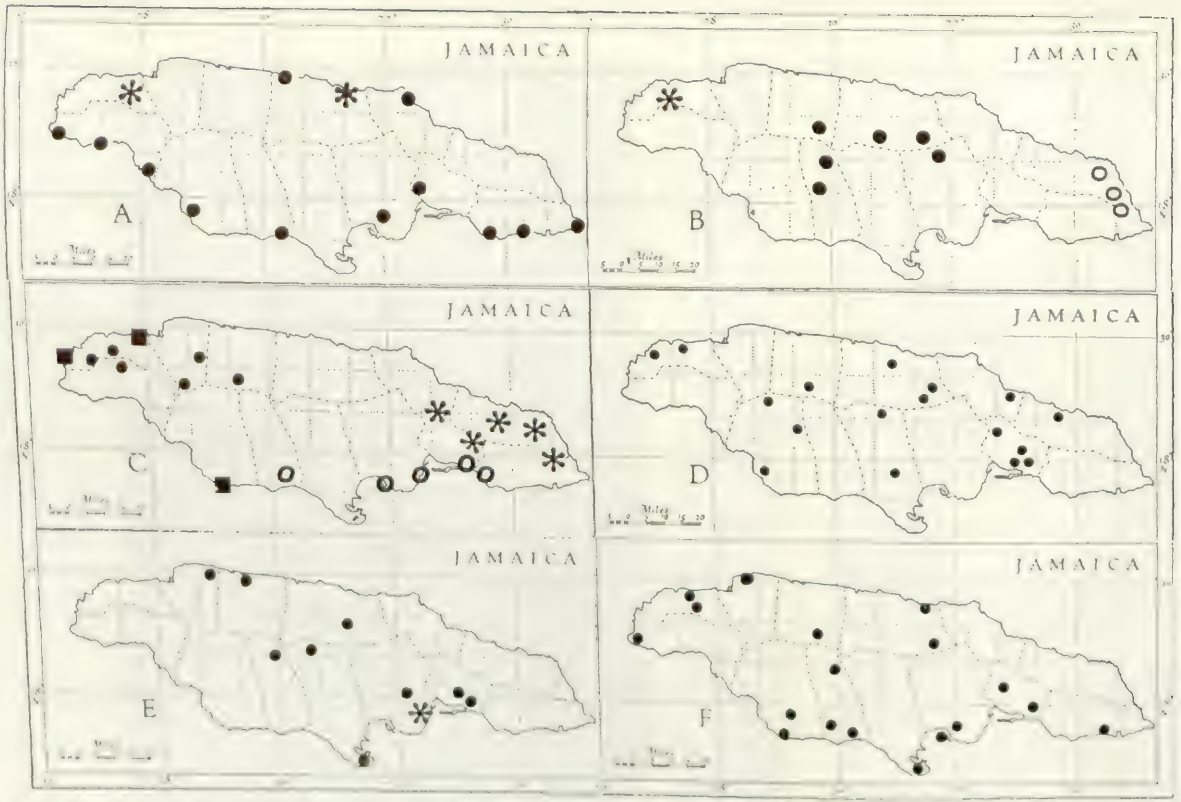

FIGURE 1. Maps showing distribution of species in Jamaica. A. *Tabernaemontana laurifolia* (dots); *T. glaucescens* (stars). B. *Tabernaemontana ovalifolia* and *T. ochroleuca* (star); *T. wullschlaegelii* (dots); *T. rendlei* (circles). C. *Tournefortia astrotricha* var. *astrotricha* (circles); *T. astrotricha* var. *subglabra* (squares); *T. staminea* (dots); *T. bicolor* (stars). D. *Tournefortia hirsutissima* (dots). E. *Bourreria baccata* (dots); *B. velutina* (star). F. *Bourreria cenosa* (dots).

Inflorescence terminal, loosely corymbose, 6–20-flowered, completely puberulous with soft erect hairs to 0.5 mm. long. *Calyx* at anthesis narrowly campanulate, about 6–7 mm. long, with acute teeth 1.5–2 mm. long, completely puberulous like the inflorescence with soft erect hairs, in fruit outspread and deeply divided with the teeth 3–4 mm. long. *Corolla* white when fresh, brown when dried, glabrous; tube about 6 mm. long; lobes broadly obovate, rounded, about 4 mm. long. *Stamens* exserted; filaments above insertion about 2.5 mm. long, anthers 2 mm. long. *Style* divided at the apex into two branches 0.5–1 mm. long. *Fruit* 7–10 mm. in diameter, red.

Jamaica. ST. CATHERINE: Port Henderson, *Lane 423* (K). Port Henderson Hill, 50–250 ft., vii. 1958, vii. 1954, *Webster & Wilson 4930* (BM; IJ). Near Port Henderson, 250 ft., xi. 1957, *Yuncker 17477* (BM); Port Henderson Hill, E. of Great Salt Pond, vii. 1958, *Powell 558* (BM; IJ).

This puberulous species has hitherto been confused with the widespread sericeous *Bourreria baccata*. Apparently it is confined to the low coastal scrub on the hot dry "dog-tooth" limestone of the Healthshire Hills of St. Catherine, which the earlier collectors Sloane, Bertero, and Lane could

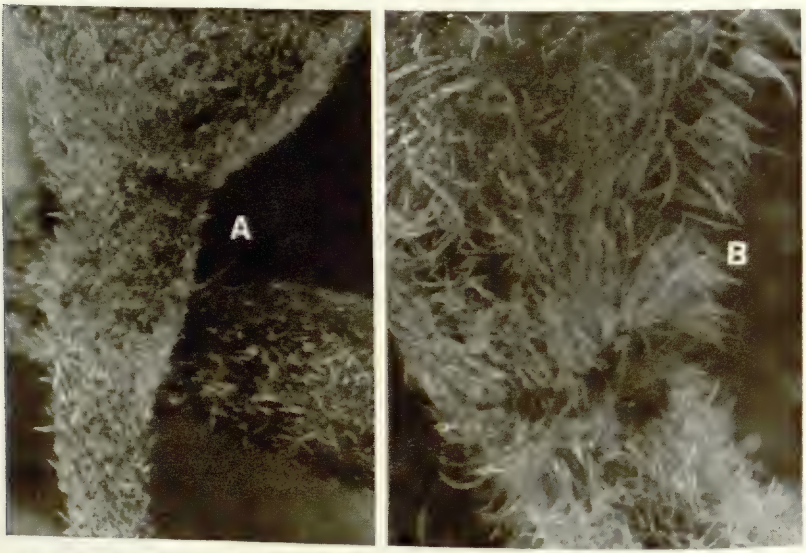

FIGURE 2. Photographs showing characteristic pubescence in species of *Bourreria*, × 40. A. *B. baccata* Raf., hair-covering of pedicel and calyx (from lectotype, *P. Browne* in Linnaean Herb. 245.2); B. *B. velutina* (DC.) Gürke, hair-covering of pedicel and calyx (from *Webster & Wilson 4930*, BM).

easily have reached by boat from Port Royal. The earliest gathering is in Sloane's herbarium vol. 7, fol. 36, lower specimen (BM), collected between December 1687 and March 1689. De Candolle described it in

1845 as *Ehretia velutina* from a specimen collected in Jamaica by Bertero. As his description would also apply to the closely related *B. baccata*, Dr. Werner Greuter kindly examined the type specimen for me in the De Candolle Prodromus Herbarium at the Conservatoire botanique, Geneva, and compared it as regards pubescence with modern Jamaican material of both taxa. He reports that "the type of *Ehretia velutina* has patent hairs on both calyces and pedicels. The type specimen is in complete agreement with some specimens from the Port Henderson area in our herbarium and especially with Yuncker 17477." This establishes conclusively that the name *B. velutina* belongs to the extremely local species with spreading hairs of which Miers published a good description from Lane's Port Henderson specimen under the name *Crematomia velutina* and not to the widespread species (*B. baccata*) to which other authors, notably O. E. Schulz, have applied it. For this reason a detailed description of *B. velutina*, sensu stricto, is given above.

3. **Bourreria venosa** (Miers) Stearn, comb. nov. FIGURE 1F.

Jasminum periclymeni folio, flore albo Sloane, Voy. Jam. Nat. Hist. 2: 96. *t. 204, f. 1.* 1725.

Crematomia venosa Miers, Ann. Mag. Nat. Hist. IV. 3: 305. 1869; Miers, Contrib. Bot. 2: 248. 1869.

Beureria velutina var. *venosa* (Miers) O. E. Schulz in Urban, Symb. Antill. 5: 63. 1911.

Also widespread in **Jamaica**, *Bourreria venosa* ranges from sea-level to 3000 ft. (900 m.) and has been collected in the parishes of HANOVER (*Britton 2252*; *Proctor 23906*; *Stearn 146*); WESTMORELAND (*Harris 10236*; *Britton & Hollick 2069, 2074*); ST. JAMES (*Proctor 23075*); ST. ELIZABETH (*Britton 1200*; *Harris 9703, 9806*; *Stearn 1034*; *Webster & Proctor 5326*); TRELAWNY (*Harris 8788*; *Howard & Proctor 14164*; *Howard, Proctor & Stearn 14658*; *Proctor 24488*; *Robbins 127*; *Webster, Ellis, & Miller 8388*); MANCHESTER (*Adams 9843*; *Harris 8239*; *Proctor 10590*); ST. ANN (*Harris 8981, Prior*); CLARENDON (*Lewis 5025*; *Webster 5112*); ST. CATHERINE (*Lewis 8937*; *Yuncker 17357*); ST. ANDREW (*Newill 2795*; *Proctor 10209*); and ST. THOMAS (*Webster & Wilson 4824*). It also occurs in the **Cayman Islands** on GRAND CAYMAN (*Brunt 1715, 2069*; *Kings GC 310*), LITTLE CAYMAN (*Proctor 28149*) and CAYMAN BRAC (*Proctor 29032*).

The type of *Bourreria venosa* is an unlocalized specimen collected in Jamaica by R. C. Alexander in 1850 (K; drawing by Miers of K specimen is in BM); a duplicate of this, in the personal herbarium retained by him but bequeathed to Kew in 1903, is labeled "Ocho Rios": hence, Ocho Rios, on the coast of St. Ann, is the type locality. It should be noted that Dr. Richard Chandler Alexander (1809–1902), who collected in Jamaica in 1849 and 1850, took the surname of Prior in 1859 on the death of a relative and his Jamaican collections are sometimes cited as those of Alexander, sometimes of Prior.

4. **Bourreria succulenta** Jacquin, Enum. Syst. Pl. Carib. 14. 1760; O. E. Schulz in Urban, Symb. Antill. 7: 55. 1911.

Mespilus americana laurifolia glabra fructu rubro mucilaginoso Commelin, Hortus Med. Amstel. 1: 153. *t. 79.* 1697.

The only localized Jamaican gatherings referable to *Bourreria succulenta* were collected in St. Andrews Parish at the Grove on a rocky hillside at 750–800 ft. (200–240 m.) by Harris (*5760, 12084*) and these may possibly belong to an aberrant form of *B. venosa* in which the style branches have failed to separate. The species is recorded from Cuba, Hispaniola, Puerto Rico, St. Croix, St. Martin, Barbuda, Antigua, Guadeloupe, Dominica, Martinique (locus classicus), St. Lucia, St. Vincent, Grenada, Barbados, Tobago, and Curaçao.

BORAGINACEAE

CORDIA SECTION VARRONIA IN JAMAICA

Cordia section VARRONIA (P. Browne) G. Don, Gen. Syst. Garden. Bot. 4: 382. 1837, consists of shrubs with small flowers clustered in dense heads or spikes. Its members in the West Indies, Mexico, and Central America south to Venezuela are the subject of a critical and detailed revision by Ivan M. Johnston, published in the *Journal of the Arnold Arboretum* 30: 85–104. 1949, in which he distinguished 16 species. In 1950 (op. cit. 31: 177–179) he added two more, both Jamaican. The few departures from Johnston's conclusions, as below, are not meant to diminish their value as a whole; Johnston's scholarly studies of tropical American Boraginaceae have provided a sound basis for all later work on the taxonomy and the nomenclature of the family.

The following is a synopsis of the Jamaican species.

1. Inflorescence cylindric, 1.5–3.5 cm. long.
   2. Leaves densely hairy on lower side. Calyx with evident short stiff hairs in upper part. ..... 1. *C. brownei.*
   2. Leaves almost glabrous on lower side or with hairs very short and inconspicuous. Calyx minutely hairy, appearing almost glabrous, except under a strong lens. ..... 2. *C. jamaicensis.*
1. Inflorescence globose.
   3. Hairs on upper side of mature leaf without conspicuously broadened bases. Peduncles mostly axillary. Calyx lobes acute, without linear appendages. ..... 3. *C. linnaei.*
   3. Hairs on upper side of mature leaf mostly with broadened and often swollen bases. Peduncles terminal or internodal. Calyx lobes elongated into linear appendages 1.5–6 mm. long.
      4. Calyx (exclusive of appendages 5–6 mm. long) about 5 mm. long. Leaves ovate to very broadly ovate. Peduncle with rusty brown hairs. Corolla about 9 mm. long. ..... 4. *C. clarendonensis.*
      4. Calyx (exclusive of appendages 1.5–2.5 mm. long) 4 mm. long. Leaves lanceolate to ovate, mostly narrowly ovate. Peduncle with whitish hairs. Corolla 4–6 mm. long.

5. Mature leaves rigid, thick, the lower side usually with deep depressions between the veins; hairs on the upper side with raised swollen bases. ..... 5. *C. bullata*.
5. Mature leaves thinner, the lower side normally flat and without depressions between the veins; hairs on the upper side without raised swollen bases. ..... 6. *C. globosa* var. *humilis*.

1. **Cordia brownei** (Friesen) I. M. Johnston, Jour. Arnold Arb. 31: 177. 1950; Stearn, Proc. Linn. Soc. London 170: 142. 1959.

Mountjolya Brownei Friesen, Bull. Soc. Bot. Genève II. 24: 180. 1933.

Jamaica. Parishes of St. Catherine, St. Andrew and Kingston, Portland, St. Thomas; also on Grand Cayman. For map of Jamaican distribution, see Stearn (op. cit.).

2. **Cordia jamaicensis** I. M. Johnston, Jour. Arnold Arb. 31: 179. 1950; Stearn, Proc. Linn. Soc. London 170: 142. 1959.

Jamaica. Parishes of St. James, St. Elizabeth, Trelawny, Manchester, St. Ann, Clarendon; for map of distribution see Stearn, loc. cit.

3. **Cordia linnaei** Stearn, sp. nov. Figure 3.

Ulmi angustifoliae facie Baccifera Jamaicensis foliis superne scabris, subtus villosis, floribus flavis perpusillis, fructu botryoide monospermo Plukenet. Almag. Bot. 393. 1696; Phytogr. 4: *t. 328. f. 5.* 1696.

Lantana corymbosa L. Sp. Pl. 2: 628. 1753, p.p. quoad synon. Plukenetii, non *C. corymbosa* (Desv.) G. Don, 1837.

Varronia lineata L. Syst. Nat. ed. 10. 916. [May–June] 1759, p.p. synon. Brownei excluso, *nomen illegit.*; L. Pl. Jam. Pug. (sist. Elmgren) 9. [Nov.] 1759; reimpr. in Amoen. Acad. 5: 394. 1760.

Cordia lineata (L.) Roemer & Schultes, Syst. Veg. 4. 464. 1819, *nomen illegit.*; I. M. Johnson, Jour. Arnold Arb. 30: 91. 1949.

Frutex 1.5–3 mm. high. *Ramuli* graciles brunneoli, juniores pilis densis erectis fulvis 0.3 mm. longis hispiduli, vetustiores pilis albidis, basibus prominentibus petiolorum foliolorum delapsorum munita. *Folia* breviter petiolata, dissita; lamina lanceolata, apice longe acuminata, margine sparse leviterque acute serrata praecipue supra medium, basi cuneata vel rotundata, 2.5–10 cm. longa, 0.8–3.5 cm. lata, nervis utroque latere costae 4 subtus parum prominulis curvatisque sub angulo 20°–40° abeuntibus, supra setis brevissimis et setis ad 0.4 mm. longis basi haud bulboso-inflatis intermixtis appressis asperula, subtus dense vel moderate pubescens; petioli 1–3 mm. longi. *Inflorescentiae* plerumque axillares; pedunculus simplex, 1–4 cm. longus, pilis densis patentibus ad 0.3 mm. longis hispidulus, quam folium subtentum multo brevior, basi petioli parte brevi persistenti articulatae adnatus, capitulo solitario globoso 3–12-floro, 4–7 mm. lato terminatus. *Calyx* cupularis, 2.5–3 mm. longus, pilis brevibus appressis vestitus, leniter lobatus, lobis 0.5 mm. longis mucronatis. *Corolla* anguste tubulosa, ca. 3–4 mm. longa, ore 1.5 mm. diametro, alba, intus sparse villosa, limbo

FIGURE 3. *Cordia linnaei* Stearn, holotype (BM), *Proctor 15789*.

parum expanso vix 1 mm. longo. *Stamina* ca. 2 mm. supra basin corollae inserta; filamenta ca. 1 mm. longa; antherae ca. 0.5 mm. longae semiexsertae. *Fructus* ca. 3 mm. longus, in vivo ruber, calyce aucto maximam partem velatus.

Type: **Jamaica**: St. Andrew, pastures behind Hope Gardens, 600–700 ft. 22. x. 1956, *Proctor 15789* (BM, holotype; IJ, isotype).

Jamaica. Parishes of St. Elizabeth (*Britton 694*); Manchester (*Harris 9434*); Clarendon (*Proctor 16714*); St. Catherine (*Proctor 7815*), St. Mary (*Proctor 20606*); St. Andrew and Kingston (*Adams 5479, Alexander 555*; *Powell 748*; *Proctor 15789, 18265*; *Yuncker 17767*); Portland (*Fredholm 3271*), and St. Thomas (*Britton 3618*; *Proctor 5535, 7425*).

For records outside Jamaica, for Cuba, Hispaniola, Mexico, and Central America to Venezuela, see Johnston, loc. cit. 91. 1949.

The seemingly paradoxical act of describing as new a species which has been known since the 17th century, but which nevertheless lacks a legitimate name, is intended to cut through the nomenclatural tangle and make a fresh start by associating a new name with a modern type specimen of known provenance. Johnston began his account of what he called *Cordia lineata* by referring to it as "a very well marked but previously unrecognized species here associated with a neglected specific name long ago proposed by Linnaeus. The plant is known only from Mexico, Central America and the northern West Indies and is to be found in herbaria mistakenly identified as *C. ulmifolia*, *C. corymbosa* or *C. polycephala*." Reluctant to give this a new name, Johnston resuscitated a very old one, which unfortunately is illegitimate.

The species concerned was known to Leonard Plukenet (1641–1706) and Patrick Browne (ca. 1720–1790) and from 1758 onwards to Carl Linnaeus (1707–1778), who had, however, seen no specimen when he drafted the account of *Lantana corymbosa* for the *Species Plantarum* 2: 628. 1753:

corymbosa 6. LANTANA foliis alternis, floribus corymbosis.†
Periclymenum rectum, salviae foliis majoribus oblongis mucronatis subtus villosis alternatim sitis, flore & fructu minoribus. *Sloan. jam.* 104. *hist.* 2. *p.* 83. *t.* 194. *f.* 3. *Raj. dendr.* 30.
Ulmi angustifoliae facie baccifera jamaicensis, foliis superne scabris, subtus villosis alternatim sitis, floribus parvis perpusillis, fructu botryoide monospermo. *Pluk. alm.* 393. *t.* 329. *f.* 5.
Habitat in Jamaica.
Refertur ex fide Sloanei; *De floris structura nulla mihi certitudo.*

Here confusion begins. This account is entirely based on the illustrated works of Sloane and Plukenet, and fortunately the specimens from which their illustrations were made are preserved in the British Museum (Natural History). The original of Sloane's illustration, drawn by Everard Kickius

in April 1701, is in Herb. Sloane (vol. 6, fol. 86) and belongs to the species later named *Cordia polycephala* (Lam.) I. M. Johnston. The original of Plukenet's illustration is also in Herb. Sloane (vol. 102, fol. 132) and belongs to the species named *C. linnaei* above and called *C. lineata* by Johnston. Since Sloane's illustration shows a corymbose inflorescence and Linnaeus states that his own entry had been inserted through the testimony of Sloane — *refertur ex fide Sloanei* — Sloane's illustration (op. cit. *t. 194, f. 3.* 1714) must be taken as the lectotype of *V. corymbosa*. However, the Linnaean epithet *corymbosa* cannot now be legitimately transferred to *Cordia*; its use is barred by *C. corymbosa* (Desv.) G. Don (1837) based on *Varronia corymbosa* Desvaux (1809); the earlier *C. corymbosa* Willd. ex Roemer & Schultes (1819) was published as a synonym and therefore is not valid.

In 1756 Patrick Browne published his *Civil and Natural History of Jamaica*. He was well acquainted with Linnaeus's works and adopted his methods except for the new binomial nomenclature. Here Browne defined on p. 172 a genus *Varronia*, now regarded as congeneric with *Cordia*, including two species. Under the first species, his *Varronia fruticosa foliis rugosis ovatis subhirsutis serratis alternis, capitulis subrotundis*, he cited as a synonym Linnaeus's *Lantana foliis alternis floribus corymbosis*, i.e. *L. corymbosa* L. (1753), and Sloane's *Periclymenum rectum* etc., i.e. its lectotype, although the plant figured (*t. 13, f. 2*) and described by him is that now called *Cordia globosa* var. *humilis* (Jacq.) I. M. Johnston. Linnaeus accepted Browne's genus *Varronia* in his *Systema Naturae*, ed. 10. 2: 916. 1759, his account being as follows:

VARRONIA. *Cal.* denticulatis recurvatis. *Drupa* nucleo 4-loculari.

lineata. A. V. fol. lanceolatis lineatis, spicis oblongis. Lantana corymbosa *Spec. pl.* 628. *Brown. jam. t.* 13. *f.* 2.

bullata. B. V. fol. ovatis venoso-rugosis, spicis globosis. *Sloan. jam. t.* 195. *f.* 1.

To be noted in this generic diagnosis is the phrase "Cal. denticulatis recurvatis": this refers to the recurved calyx lobes characteristic of *V. globosa*, mentioned by Browne as having "limbus in quinque lacinias tenuissimas longas reflexas vel intortas divisas" and shown in his figure. They are lacking in the species described above as *C. linnaei*.

The Linnaean epithet *lineata* used here under *Varronia* is an illegitimate substitute for *corymbosa* used earlier under *Lantana*, even though its application embraced a third species (*C. globosa* var. *humilis*), and accordingly it has the same type.

Later, in November 1759, Elmgren defended a Linnaean dissertation, *Plantarum Jamaicensium Pugillus*, intended to amplify the meager references to Jamaican plants in the *Systema Naturae*, using Patrick Browne's specimens which Linnaeus had bought in 1758. This dissertation gives, under the name *Varronia lineata*, a detailed description of the plant described above as *C. linnaei*, which is represented in Linnaeus's herbarium by specimen 255.1 (IDC. Microfiche no. 143), but no reference to Pluke-

net's figure. Actually Patrick Browne had collected three species, i.e. *C. linnaei*, *C. bullata*, and *C. globosa* var. *humilis*.

In the second edition (1762) of the *Species Plantarum* Linnaeus completely altered the earlier concept which he had called *Lantana corymbosa*. This now became *Varronia lineata*, with the original *C. corymbosa* as a synonym but with a new diagnosis, a citation of Plukenet's figure and a citation of the Elmgren dissertation. Thereby, in Johnston's opinion, Linnaeus restricted the application of the epithet *lineata* to the species here called *C. linnaei* but he did not in so doing make the illegitimate epithet *lineata* legitimate. Johnston accepted Plukenet's plate (not Sloane's) as typifying both *Lantana corymbosa* and *Varronia lineata* and he adopted the name *Cordia lineata* published by Roemer and Schultes in 1819.

Since the species concerned (*C. linnaei*) had no legitimate name under *Cordia* in 1819, Roemer and Schultes's use of the name *Cordia lineata* might be regarded as publication of a new name starting from 1819 instead of a new combination based on an illegitimate name of 1759. Unfortunately they cited as synonyms *Varronia humilis* Jacq. and *V. polycephala* Lam., which provided epithets they could have adopted at that time in accordance with their taxonomy although in fact these epithets relate to different species; consequently their name *C. lineata* is also illegitimate.

The next possible name seemed to be *Cordia adnata* DC., Prodromus 9: 493. 1845, based on a specimen of uncertain origin. However, a photograph of the type in the Prodromus Herbarium at Geneva shows a plant with several-headed peduncles, as well as slightly larger heads and less acuminate leaves than *C. linnaei*, agreeing in habit with specimens of *C. polycephala* from Puerto Rico.

Since Johnston's "Cordia lineata," therefore, appears to have no legitimate name I have accordingly named it *C. linnaei* both to maintain it in the same alphabetical sequence and to recall the references to it in the works of Carl Linnaeus.

4. **Cordia clarendonensis** (Britton) Stearn, comb. nov.

Varronia clarendonensis Britton, Bull. Torrey Bot. Club **41**: 16. 1914; Friesen, Bull. Soc. Bot. Genève II. **24**: 155. 1933.

Jamaica. Parish of CLARENDON, at Peckham Woods, 760 m., where Harris (no. *10995*) collected it in July, 1911.

5. **Cordia bullata** (L.) Roemer & Schultes, Syst. Veg. **4**: 462. 1819; I. M. Johnston, Jour. Arnold Arb. **30**: 96. 1949.

Periclymenum rectum, salviae folio rugoso majore, subrotundo, bullata Sloane Cat. Pl. Jam. 163. 1696; Voy. Jam. **2**: *t. 195, f. 1*. 1725.

Varronia bullata L. Syst. Nat. ed. 10. **2**: 916. [June] 1759; L. Fl. Jam. Pub. (sist. Elmgren) 9 (Nov. 1759); reimpr. in Amoen. Acad. **5**: 394. 1760.

Jamaica. Parishes of ST. JAMES, TRELAWNY, ST. ELIZABETH, MAN-

CHESTER, CLARENDON, ST. ANN, ST. CATHERINE, KINGSTON and ST. ANDREW, ST. THOMAS.

6. **Cordia globosa** (Jacq.) Kunth, Nova Gen. 3: 76. 1818.
Var. **humilis** (Jacq.) I. M. Johnston, Jour. Arnold Arb. **30**: 98, 116. 1949.

Periclymenum rectum, salviae folio rugoso minore bullato, flore albo Sloane, Cat. Pl. Jam. 163. 1696; Voy. Jam. **2**: 81. *t. 194. f. 2.* 1725.

Varronia fruticosa foliis rugosis ovatis subhirsutis serratis alternis, capitulis subrotundis Browne, Hist. Jam. 172. *t. 13, f. 2.* 1756.

Varronia humilis Jacq. Enum. Pl. Carib. 14. 1760; Select. Stirp. Amer. 41. 1763.

Cordia humilis (Jacq.) G. Don, Gen. Syst. Garden. Bot. **4**: 383. 1837.

Florida, Cuba, Cayman Islands, Jamaica (all parishes), Hispaniola, Mexico, Guatemala, Salvador, Nicaragua, Panama.

Cordia globosa is a widely ranging species of which the nomenclatural type probably came from the lesser Antilles; the name *C. globosa* var. *globosa* is accordingly used for the southern geographical race distinguished by Johnston and stated to range over the lesser Antilles, Venezuela, and Brazil.

TOURNEFORTIA

Tournefortia astrotricha DC. Prodr. **9**: 520. 1845; Griseb., Fl. Brit. W. Ind. Isl. 483. 186.
Var. **astrotricha.**

Tournefortia astrotricha was described by De Candolle from a specimen collected in 1821 by Carlo Giuseppe Bertero (1789–1831) in Jamaica, probably on the Long Mountain west of Kingston. It has relatively large leaves, up to 20 cm. long and 11 cm. broad, densely hirsute below with curved hairs spreading in all directions and sometimes appearing stellately arranged, whence the epithet *astrotricha*, as indicated by De Candolle's description of the leaves "subtus pube conferta stellatim disposita sericeo-tomentosis pallidis."

It grows in dry rocky places along the southern coast of Jamaica in the parishes of ST. THOMAS (*Adams 5493*); ST. ANDREW and KINGSTON (*Harris 8930*; *Graham 8047*; *Campbell 6413*; *Stearn 832*; *Webster & Wilson 4851*; *Webster et al. 8374*; *Yuncker 17,750*); ST. CATHERINE (*Britton & Hollick 1833*; *Harris 9330*); CLARENDON (*Lewis & van der Porten 3134*; *Lewis 2447*; *Howard 12002*); and MANCHESTER (*Proctor 27539*). It reappears in the Cayman Islands on GRAND CAYMAN (*Kings G.C. 155*; *Kings G.C. 343*; *Proctor 11999, 15041*).

In St. Elizabeth and on the northwest coast in Hanover and St. James a very similar plant to *Tournefortia astrotricha* occurs which has relatively few hairs on the lower leaf surface. Before visiting Jamaica, I had de-

scribed this (though not published it) as a new species confined to the vicinity of Montego Bay. Specific rank now seems too high for it.

Var. **subglabra** Stearn, var. nov.

Folia subglabra, subtus pilis sparsis brevibus plusminusve appressis munita.

Shrub of straggling sparse habit up to 5 m. (15 ft.) high; branchlets stout, those of current year sparsely pubescent, of previous year glabrous and prominently bossed with leaf-scars, later furrowed. *Leaves* short-stalked; blade narrowly ovate to narrowly elliptic, the apex acute, the margin entire, the base narrowly cuneate, 2.5–20 cm. long, 1.5–8 cm. broad, both sides glabrous except for a few scattered curved appressed hairs, the primary veins in 7 to 9 pairs; petiole 0.5–1 cm. long. *Inflorescence* several times branched, many flowered, sparsely pubescent with short more or less appressed hairs, the ultimate branches 4–20 cm. long. *Calyx* about 2.2–5 mm. long, green; segments lanceolate, sparsely pubescent. *Corolla* scented; tube green, glabrous in the lower half, minutely strigose in the upper half, about 4–6 mm. long; limb 5-parted, about 3–4 mm. across, white becoming reddish, with the segments suborbicular, about 2 mm. long, 2–4 mm. broad. *Anthers* about 1.2 mm. long, inserted about 2.2–2.5 mm. above the base of the corolla tube. *Gynoecium* about 2.5–3 mm. long; stigma about 1 mm. broad, mounted on an evident style about 1.5 mm. long. *Fruits* subglobose, in the dried state about 4 mm. long and broad, when fresh to 7 mm. long and 9 mm. broad, white, not blotched.

Jamaica. HANOVER or ST. JAMES: Montego Bay to Round Hill Bluff, 25. iii. 1908, *Harris 10351* (BM, K, isotypes; NY, holotype). Near the mouth of Great River, west of Montego Bay, sea-level, 30. iii. 1920. *Maxon & Killip 1431* (NY). HANOVER: Orange Point, 100 ft., 7. iv. 1963. *Proctor 23475* (BM). ST. ELIZABETH: Great Pedro Bluff, 50 ft. 11. v. 1956, *Stearn 1029* (A; BM).

GRAND CAYMAN: near Beach Club Hotel, West Bay Road, Georgetown, 8. vi. 1967, *Brunt 2080* (BM).

Probably the Grand Cayman plant collected by Brunt has been independently evolved from *T. astrotricha* var. *astrotricha* there, and not directly derived from the western Jamaican population.

Tournefortia astrotricha belongs to a group of species with rather large leaves, i.e. on flowering shoots at least 8 cm. long and 3.5 cm. broad and sometimes up to 30 cm. long and 8 cm. broad, and suborbicular or oblong corolla lobes about as long as broad. The Jamaican species, i.e. *T. astrotricha* DC., *T. bicolor* Swartz, *T. hirsutissima* L. and *T. staminea* Griseb., may be distinguished as follows:

1. Anthers with their tips protruding from the mouth of the corolla. . . . . *T. staminea.*

1. Anthers completely enclosed within the corolla tube, their tips not protruding.
   2. Stigma almost or quite sessile on the ovary.

3. Hairs of corolla 6–8 mm. long, very abundant. Leaves very hairy. ..... *T. hirsutissima.*
3. Hairs of corolla 4 mm. or less long, fewer. Leaves almost or quite glabrous. ..... *T. bicolor.*

2. Stigma mounted on an evident style or prolongation of the ovary 1–1.5 mm. long. ..... *T. astrotricha.*
4. Leaves densely hairy beneath. ..... var. *astrotricha.*
4. Leaves very sparsely hairy beneath. ..... var. *subglabra.*

These taxa have distinctive ranges (FIGURE 1 C and D). Thus *Tournefortia astrotricha* is exclusively coastal, while *T. staminea* inhabits the western upland and montane region at 800 ft. (240 m.) to 1600 ft. (480 m.) in the parishes of Hanover, Westmoreland, St. James, and Trelawny, and *T. bicolor* the eastern region at 1000 ft. (300 m.) to 3500 ft. (1060 m.) in the parishes of St. Mary, St. Andrew, Portland, and St. Thomas. The "chiggernut," *T. hirsutissima*, probably occurs in every parish and ranges from sea-level to 700 m.

SOLANACEAE

SOLANUM*

Solanum americanum Miller, Gard. Dict. ed. 8, art. *Solanum* no. 5. 1768.

Var. **nodiflorum** (Jacq.) Edmonds, comb. et stat. nov.

Solanum nodiflorum Jacq. Coll. Bot. 2: 288. 1789; Icon. Pl. Rar. 2: *t. 326.* 1789.

Revision of the South American taxa of *Solanum* L. sect. SOLANUM (§ *Maurella* Nees, § *Morella* (Dunal) Bitter) typified by *S. nigrum* L. has made apparent the need to reduce to synonymy very many specific names proposed for members of this complex group. I regard *S. americanum* Miller and *S. nodiflorum* Jacquin as conspecific. Early authors placed them in *S. nigrum* L., sensu lato, which breaks up, however, into a number of taxa, distinguishable on correlated morphological and cytological features, which can be reasonably treated as species. The name *S. nigrum* can then be restricted to a hexaploid taxon (with $2n = 72$) while the name *S. americanum* is used for a diploid taxon (with $2n = 24$). *S. americanum* as here interpreted is represented in the eastern half of South America, including the whole of Brazil, by glabrescent plants and in the western half by finely pubescent plants. Miller described his *S. americanum* from plants cultivated in the Chelsea Physic Garden and said to have been introduced from Virginia. The cultivated specimen from Miller's herbarium in the British Museum (Natural History), London, agrees with his description as far as it goes and is finely pubescent. Jacquin described and illustrated *S. nodiflorum* from plants cultivated at Vienna and stated to have been introduced from Mauritius. This species is represented by

* By Jennifer M. Edmonds.

a specimen from Jacquin cultivated in Vienna, now in the British Museum (Natural History) which is glabrescent; Professor G. T. S. Baylis recorded (in Trans. Roy. Soc. New Zealand **85**: 381. 1958) the mean diameter of the pollen (mounted in lactophenol blue) of this specimen as 23μ. The two types agree in all essential floral and vegetative features. Accordingly the name *S. americanum* has, on grounds of priority, to be adopted as the earliest specific name available for plants of the diploid group within the *S. nigrum* complex hitherto distinguished as *S. nodiflorum*. Jamaican specimens, being glabrescent, belong to var. *nodiflorum*.

The differences separating *Solanum americanum* from *S. nigrum*, sensu stricto, are collectively significant. Thus *S. americanum* has smaller flowers with the corolla 5–9 mm. across and anthers ca. 1–2 mm. long, erect fruiting pedicels, glossy globose berries 5–7 mm. wide with constantly well reflexed sepals and smaller seeds (only 1–1.5 mm. long), as well as smaller pollen grains associated with its diploid state. *S. nigrum* has larger flowers with the corolla 10–18 mm. across and anthers (1.5–)2.7 mm. long, dull black or green ovoid berries 6–10 mm. wide with the sepals often appressed to them or else moderately reflexed, and larger seeds (1.7–2.4 mm. long).

The mean diameters of pollen grains of Jamaican species of *S. americanum* var. *nodiflorum* collected by Stearn, measured by Baylis after mounting in lactophenol blue and recorded on the sheets (BM) are *Stearn 113*, 23.0μ (21.5–23.7μ), *181*, 24.3μ (23.7–25.8μ), *271*, 22.1μ (21.5–23.7μ), *330*, 23.4μ (21.5–23.7μ), *365*, 24.1μ (21.5–28.0μ), *432*, 19.8μ (19.4–21.5μ), *483*, 21.3μ (19.4–21.5μ), *584*, 23.9μ (23.7–25.8μ). The anthers on these specimens vary from 1.0 to 1.7 mm. but are mostly 1.5 mm. long. These measurements fit in with Baylis's finding in New Zealand material of *nodiflorum* a mean pollen diameter of 21μ and a range of 20–27μ. Baylis found the range of pollen diameter in *S. nigrum*, similarly mounted in lactophenol blue, to be 27–38μ.

SCROPHULARIACEAE

Alectra fluminensis (Vell.) Stearn, comb. nov.

Pedicularis melampyroides Richard, Actes Soc. Hist. Nat. Paris **1**: 111. 1792.
Scrophularia fluminensis Vellozo, Fl. Flumin. 263. 1825; Fl. Flumin. Ic. **6**: *t. 87*. 1831.
Alectra brasiliensis Benth. in DC. Prodr. **10**: 339. 1846; Griseb. Fl. Brit. W. Ind. Isl. 429. 1862; J. A. Schmidt in Mart. Fl. Bras. **8**(1): 273. *t. 47*. 1862.
Alectra melampyroides (Rich.) Kuntze, Rev. Gen. Pl. **2**: 458. 1891; Melchior, Notizbl. Bot. Gart. Berlin **15**: 435. 1941, non *A. melampyroides* Benth. 1846.
Melasma brasiliense (Benth.) Chodat & Hassler, Bull. Herb. Boiss. II. **4**: 291. 1904.
Melasma melampyroides (Rich.) Pennell ex Britton & Wilson, Sci. Surv. Porto Rico Virgin Is. **6**: 188. 1925; R. E. D. Baker in Fl. Trinidad & Tobago **2**: 285. 1954.

This species has long been known from Puerto Rico, the Lesser Antilles, and Trinidad and is apparently widespread in northern South America

(Guyana, Venezuela, Brazil, Paraguay) but was first found in Jamaica, in Hanover parish on Dolphin Head, in 1960 by Dennis Adams (*no. 8641*) and later in Westmoreland parish at Seedy Pond, southeast of Mount Grace, in 1966 by George Proctor (*no. 27703*). Vellozo's epithet *fluminensis* refers to Rio de Janeiro (*Flumen Januarii*), Brazil.

Although *Melasma* Bergius (1767) and *Alectra* Thunb. (1784) have from time to time been treated as congeneric, H. Melchior in his papers, "Beitrag zur Kenntnis der Gattung *Melasma*" (Notizbl. Bot. Gart. Berlin **15**: 119–127. 1940) and "Die Gattung *Alectra* Thunb." (loc. cit. 423–447. 1941), has provided reason to keep them apart.

ACANTHACEAE

JUSTICIA

The definition of the genus *Justicia* L. and the typification of its name provide interlocked problems of taxonomy and nomenclature for which every possible solution is certain to cause nomenclatural disturbance. As commonly accepted, e.g. by E. C. Leonard (Contr. U. S. Natl. Herb. **31**: 487–645. 1958), R. W. Long (Jour. Arnold Arb. **51**: 302–309. 1970) and the authors of most Floras, *Justicia* includes some 300 species found in both the Old World and the New, especially in South America, and manifests great diversity in habit, inflorescence, corolla, anthers, and pollen. Emphasis on this diversity led C. G. D. Nees von Esenbeck (1776–1858), who possessed an extraordinarily wide and detailed knowledge of the *Acanthaceae*, to divide the group into smaller genera such as *Adhatoda*, *Amphiscopia*, *Beloperone*, *Gendarussa*, *Leptostachya*, *Orthotactus*, *Rhapidospora*, *Rhytiglossa*, and *Rostellularia*, most of which have been merged again in *Justicia* by other authors. Nees knew nothing about the markedly different types of pollen within the family which Radlkofer and Lindau later emphasized and used taxonomically; nevertheless many of his groups were restored to generic status by Bremekamp (e.g. in Verhandl. Kon. Nederl. Akad. Wet. Natuurk. II. **45**(2): 43–61. 1948) after diligently studying their pollen. Bremekamp's work indicates the lines along which *Justicia*, sensu lato, could be divided; it covers, however, relatively few species. Moreover logical application of his concepts to them all, a vast and difficult task, would result in almost every species now called a *Justicia* being called something else. Accordingly, until correlations between differences in inflorescence, floral characters, pollen, and seeds have been established throughout its range and relatively homogeneous natural groups have consequently been defined, the simplest course is to maintain *Justicia* as a large genus while recognizing the possibility of its later dismemberment and the revival of names now buried in its synonymy. This avoids or at least postpones the awkward consequences of typification, associated with narrow generic concepts which become evident on examining its history.

The name *Justicia* was first used by Linnaeus in 1737 (Genera Plan-

tarum 4, no. 12). His heading reads "JUSTICIA *Houst.* A. A. Adhatoda *Tournef.* 79. Ecbolium *Riv.* 1. 129." The cryptic "*Houst.* A. A." refers to an intended publication on new genera by William Houstoun (1695–1733). Made acquainted with Houstoun's manuscript and drawings by Philip Miller, Linnaeus expected this would form part of the *Philosophical Transactions* of the Royal Society of London, the title of which he latinized as *Acta Anglica* and then abbreviated to "A. A.," but Houstoun's work was not published until 1781, after the death of all concerned, by Sir Joseph Banks under the title *Reliquiae Houstounianae*. Houstoun based his genus *Justicia* on American species now placed in the genus *Dicliptera*. Linnaeus took from him only the name *Justicia* commemorating Houstoun's fellow countryman James Justice (d. 1762 or '63), Clerk of the Sessions at Edinburgh. He based his own generic description in the *Genera Plantarum* on the Asiatic species later named *Justicia adhatoda* L. (*Adhatoda zeylanica* Med.), merely substituting the name *Justicia* for Paul Hermann's *Adhatoda* used by Tournefort (Inst. Rei Herb. 175. *t.* 79. 1700), because this was derived from the Tamil vernacular name "Adathodai," Sinhalese "Adathoda," meaning "goat not touch," in allusion to its bitter leaves, and Linnaeus rejected such *nomina Barbara*. His reference "Riv. 1. 129" is to a plate under the name *Ecbolium* in Rivinus, *Icones Plantarum, quae sunt Florae irregulari monopetalo* (1690), which illustrates *Justicia adhatoda* received from Paul Hermann (cf. Rivinus, Introd. 16. 1690). The same generic description was repeated in the fifth edition of the *Genera Plantarum* (10. no. 26. 1754) with added details of the pistil. The historic type of *Justicia* L. is thus *J. adhatoda* and Britton in 1918 (Fl. Bermuda 54) designated this as its lectotype, thereby making *Justicia*, sensu stricto, equivalent to *Adhatoda* Miller.

In the *Species Plantarum* (1753) Linnaeus expanded his concept of the genus *Justicia* to include ten other species, although he did not emend his generic description in the *Genera Plantarum* (1754) to fit them. Indeed these species differ so much among themselves that later authors have put them in different genera as indicated below.

1. *J. Adhatoda*: later *Adhatoda zeylanica* Medicus, 1790; *A. vasica* Nees, 1832.
2. *J. Ecbolium*: later *Ecbolium viride* (Forsk.) Alston: *E. linneanum* Kurz, 1871.
3. *J. Betonica*: later *Adhatoda betonica* (L.) Nees, 1832.
4. *J. hyssopifolia*: later *Gendarussa hyssopifolia* (L.) Webb & Berth., 1845.
5. *J. procumbens*: later *Rostellularia procumbens* (L.) Nees, 1847.
6. *J. repens*: later *Rungia repens* (L.) Nees, 1832.
7. *J. chinensis*: later *Dicliptera chinensis* (L.) Juss., 1807.
8. *J. echioides*: later *Andrographis echioides* (L.) Nees, 1832.
9. *J. sexangularis*: later *Dicliptera sexangularis* (L.) Kurz, 1870.
10. *J. nasuta*: later *Rhinacanthus nasutus* (L.) Kurz, 1870.
11. *J. purpurea*: later *Hypoestes purpurea* (L.) Solander ex Roem. & Schultes, 1817.

Of these species only 1 (*adhatoda*), 4 (*hyssopifolia*), and 9 (*sexangularis*) were known to Linnaeus when preparing his *Hortus Cliffortianus* (1738);

he became acquainted with 2 (*Ecbolium*), 3 (*Betonica*), 5 (*procumbens*), 6 (*repens*), and 8 (*echioides*) when preparing his *Flora Zeylanica* (1747) and with 7 (*chinensis*), 10 (*nasuta*), and 11 (*purpurea*) when preparing his *Species Plantarum* (1753). Linnaeus's generic description excludes 9 (*sexangularis*). Unfortunately 1 (*Adhatoda*) belongs to a little group often separated generically, as *Adhatoda* Miller, from *Justicia* as commonly interpreted.

Acceptance, following Britton, of *Justicia adhatoda* as lectotype of *Justicia* means that for those botanists who also maintain this generic separation, accepted reluctantly by H. Heine (Fl. Gabon 13: 173. 1966) but described by him as artificial, disputable, and based on a character of feeble taxonomic value, all but about 10 of the 300 or so species now in *Justicia* must be placed under other generic names.

Hitchcock and Green proposed in 1929 (Int. Bot. Congr., Cambridge, Nom. Prop. Brit. Bot. 116) the acceptance as standard-species (lectotype) of "*J. hyssopifolia*, the best known of the four species now retained in the genus." However, this does not accord well with most species currently placed in *Justicia* either. *J. hyssopifolia* is a remarkable shrubby Canarian species, on which Webb & Berthelot based their *Gendarussa* subgenus DIPSAS; this and a few allied African species could well form a separate genus if one adopted narrow generic concepts in the group. The consequence would again be the transfer of most of the species now in *Justicia* into other genera, but in the absence of any available subdivision of *Justicia*, sensu lato, into acceptable groups no one would know where else to put them. Bremekamp, in 1948 proposed the restriction of *Justicia* to *J. hyssopifolia* and its close allies, used the Linnaean name *Dianthera* for a small group of American species, the names *Beloperone* Nees, *Psacadocalymma* Bremek. (a synonym of *Stethoma* Raf.) and *Calliaspidia* Bremek. (a synonym of *Drejerella* Lindau) for a few others, and noted that *J. carthaginensis* and its allies would then have to be transferred to a genus of their own as yet unnamed, but he necessarily left the major world-covering problems almost untouched since he was primarily concerned with the Acanthaceae of Java.

It is indeed comparatively easy to arrange the *Justicia* species of a limited area into natural groups equivalent to accepted genera, but how universally valid are the distinctions thus made on a regional basis? If narrow generic concepts are adopted in this group, none of the American species belongs to *Justicia*, sensu stricto; then, for example, the 71 species described from Colombia by Leonard would be of uncertain generic allocation, and the same applies to most African and Asiatic species currently included in *Justicia*.

Maintenance of *Justicia* as a large genus means, however, that *Beloperone* and *Drejerella* cannot logically be excluded from it. Lindau founded his genus *Drejerella* in 1900 (Urban, Symb. Antill. 2: 222) to include three West Indian species, *D. mirabilioides* (*Justicia mirabilioides* Lam.),

D. nemorosa (*J. nemorosa* Swartz) and *D. origanoides* (*Adhatoda origanoides* Nees, *J. origanoides* (Nees) Griseb. non Vahl) and two Mexican species, *D. virgata* (*Drejera virgata* Oerstedt) and *D. fulvicoma* (*Justicia fulvicoma* Schlecht.). He placed it in a group of genera with "Spangenpollen," i.e. with 3-pored pollen grains having each pore flanked by a narrow raised longitudinal band. *Justicia*, *Jacobinia*, and *Beloperone* formed a separate group with "Knötchenpollen," having the pores flanked on each side not by a simple raised band defined by the pore-furrow (colpus) and an outer furrow (pseudocolpus), but by one to three longitudinal rows of low protuberances or raised dots (insulae), one row in *Justicia*, two in *Beloperone*, two or three in *Jacobinia*. These distinctions need amendment, if accepted at all. *Drejerella* is indeed a natural group with large overlapping bracts and 3-pored pollen but, although in *D. origanoides* and in *D. tomentosula* Urban the band or ridge on each side of the pore is entire, in *D. blechoides* Lindau, *D. fulvicoma* (*Beloperone pringlei* S. Watson), *D. guttata* (Brandeg.) Bremek. and *D. mirabilioides*, lectotype of *Drejerella*, it is replaced by a single row of 9 to 12 protuberances. The type species of *Beloperone* Nees, *B. brasiliana* (Roth) Bremek. (*B. amherstiae* Nees), has 2-pored pollen, with two or three rows of 8 to 10 protuberances each side of the pore. Similar 2-pored pollen with two rows of protuberances each side of the pore occurs in *Justicia carthaginensis* Jacq. and *J. eustachiana* Jacq. (placed in *Beloperone* by Lindau). The two possible lectotypes for *Justicia*, as explained above, *J. adhatoda* and *J. hyssopifolia*, both have 2-pored pollen. In *J. adhatoda* there is a faint row of protuberances each side of the pore, in *J. hyssopifolia* an entire band. A possible separation simply on the number of pores, i.e. two pores in *Justicia* (including *Adhatoda*, *Beloperone*, *Dianthera*, and *Stethoma*), three in *Drejerella* (including *Calliaspidia*) would, however, merely produce two artificial assemblages so heterogeneous in other characters as to need further subdivision, for which not enough information is available at present. Three-pored pollen occurs in the Asiatic *Justicia betonica*, *J. gendarussa* Burm. f., and *J. ventricosa* Hook. and, if *Justicia* is restricted to species with 2-pored pollen, then these should be removed from it, together probably with other Asiatic species not related to the American *Drejerella* species. However, much diversity exists among pollen grains with two pores. In *J. comata*, for example, the pore is flanked either by three protuberances or an almost entire band. The palynology of the group as a whole must certainly have a significant part in its reclassification. Pending that reclassification, *Justicia* is probably best accepted in a broad sense. Its Jamaican representatives may be distinguished as follows:

1. Inflorescence diffuse, with numerous very slender branches. Bracts inconspicuous, not more than 2 mm. long. Corolla less than 1 cm. long. Low-growing herbs. Pollen grains 2-pored, with 3–4 protuberances each side of the pore.
   2. Corolla 3–5 mm. long. Inflorescences axillary and terminal; the branches mostly whorled (i.e. 3–7 arising at the same level). . . . . *J. comata*.

2. Corolla 7–9 mm. long. Inflorescences mostly terminal, the lower branches paired or alternate (i.e. arising only 2 together or else singly at different levels). ..... *J. pectoralis.*

1. Inflorescence short, dense, stout. Bracts conspicuous, overlapping, the lowermost about 1–4 cm. long. Corolla 2.5–4 cm. long. Shrubs or subshrubs.
   3. Inflorescences axillary on peduncles 5–10 cm. long. Corolla with distinctly curved upper lip. Pollen grains 2-pored. Naturalized in Jamaica. ..... *J. adhatoda.*
   3. Inflorescences terminal or, if axillary, then peduncle not more than 2 cm. long. Corolla with straight upper lip.
      4. Bracts of inflorescence gradually narrowed to the base, oblanceolate. Pollen grains 2-pored. Cultivated in Jamaica. ..... *J. carthaginensis.*
      4. Bracts of inflorescence rounded or broadly cuneate at base, lanceolate, narrowly ovate, elliptic or rotund. Pollen grains 3-pored.
         5. Inflorescence drooping or horizontal. Corolla white with red markings on lips. Cultivated in Jamaica. ..... *J. brandegeana.*
         5. Inflorescence erect or ascending. Corolla pink, crimson, or purple.
            6. Shoots densely covered with spreading hairs to 2 mm. long. Petioles always very short (4–10 mm. long). ... *J. jamaicensis.*
            6. Shoots almost glabrous or inconspicuously hairy with very short hairs.
               7. Leaves acuminate. Bracts lanceolate or narrowly ovate, acute. Corolla to 3 cm. long. ..... *J. nemorosa.*
               7. Leaves obtuse or acute. Bracts rotund to elliptic, rounded or abruptly acute. Corolla 3.5–4 cm. long. ... *J. blechoides.*

Justicia adhatoda L. Sp. Pl. 1: 15. 1753; Lindau in Urban, Symb. Antill. 2: 234. 1900.

Justicia arborea, foliis lanceolato-ovatis, bracteis ovatis persistentibus, corolla galea concava L. Fl. Zeyl. 6. 1747.

Adhatoda zeylanica Medicus in Hist. Comm. Acad. Theod. Palat. 6. Phys.: 393. 1790.

Adhatoda vasica Nees in Wall. Pl. Asiat. Rar. 3: 103. 1832.

A native of India and Ceylon often cultivated in tropical gardens, this is naturalized in Jamaica in the parish of St. Thomas.

Justicia blechoides (Lindau) Stearn, comb. nov. FIGURE 4C.

Drejerella blechoides Lindau in Urban, Symb. Antill. 6: 43. 1909.

Jamaica. Parish of TRELAWNY (*Adams 6735*; *Harris 8958, 9356, 10663*; *Proctor 15755*).

Justicia brandegeana Wassh. & L. B. Smith in Reitz, Fl. Illustr. Catarin. Acant.: 102. 1969.

Beloperone guttata Brandegee in Univ. Calif. Publ. Bot. 4: 278. 1912, non *Justicia guttata* Wall.

Calliaspidia guttata (Brandegee) Bremek. in Verh. Kon. Nederl. Akad. Wet. Natuurk. II. 45(2): 54. 1948.

Drejerella guttata (Brandegee) Bremek. in Philipp. Jour. Sci. 80: 14. 1952.

A native of Mexico, commonly cultivated under the name "Shrimp plant," this is grown in Jamaica but has not been reported anywhere as naturalized.

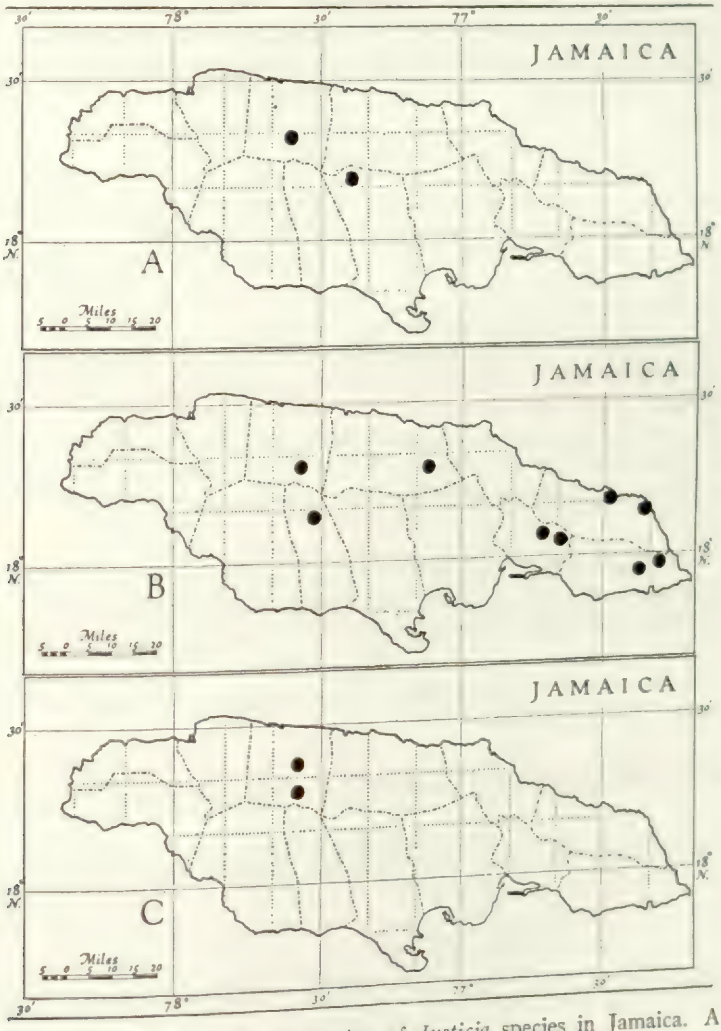

FIGURE 4. Maps showing distribution of *Justicia* species in Jamaica. A. *J. jamaicensis*; B. *J. nemorosa*; C. *J. blechoides*.

Justicia carthaginensis Jacq. Enum. Pl. Carib. 11. 1760; Select. Stirp. Am. 5. *t. 5.* 1763; Lindau in Urban, Symb. Antill. 2: 234. 1900.

Adhatoda carthaginensis (Jacq.) Nees in DC. Prodr. 11: 403. 1846.
Ecbolium carthaginense (Jacq.) O. Kuntze, Rev. Gen. Pl. 1: 980. 1891.

Recorded in error from Jamaica. Widespread in the West Indies and

Middle America south to Venezuela, its type locality, but known in Jamaica only as a cultivated plant.

Justicia comata (L.) Lam. Encycl. Méth. Bot. **1**: 632. 1785; Swartz, Obs. Bot. 14. 1791.

Antirrhinum minus angustifolium, flore dilute purpureo Sloane, Cat. Pl. Jam. 59. 1696; Voy. Jam. **1**: 60. *t. 103, f. 2.* 1707.
Dianthera foliis lanceolato-ovatis etc. Browne, Hist. Jam. 118. 1756.
Dianthera comata L. Syst. Nat. ed. 10. **2**: 850. 1759.
Justicia humifusa Swartz, Prodr. 14. 1788; Fl. Ind. Occ. **1**: 35. 1797.
Leptostachya comata (L.) Nees in DC. Prodr. **11**: 381. 1847.
Ecbolium comatum (L.) Kuntze, Rev. Gen. Pl. **1**: 487. 1891.
Stethoma comata (L.) Britton in Sci. Surv. Porto Rico Virgin Is. **6**: 218. 1925.
Psacadocalymma comatum (L.) Bremek. in Verh. Kon. Nederl. Akad. Wet. Natuurk. II. **45**(2): 55. 1948.

Jamaica. Parishes of HANOVER, WESTMORELAND, ST. JAMES, TRELAWNY, CLARENDON, ST. ANN, ST. CATHERINE, ST. MARY, ST. ANDREW, PORTLAND.

This species is widespread in the West Indies, where it grows in moist places, mostly at the edges of ponds and along irrigation trenches, and also extends from British Honduras and Guatemala to Colombia.

Justicia jamaicensis (Britton) Stearn, comb. nov. FIGURE 4A.

Jacobinia? jamaicensis Britton in Bull. Torrey Bot. Club **41**: 16. 1914.
Drejerella jamaicensis (Britton) S. Moore in Jour. Bot. (London) **65**: 221. 1927.

Jamaica. Parishes of TRELAWNY (*Proctor 11051*); CLARENDON (*Harris 10978, 11178, 12783*).

Justicia nemorosa Swartz, Prodr. 14. 1788; Fl. Ind. Occ. **1**: 37. 1797. FIGURE 4B.

Beloperone nemorosa (Swartz) Nees in DC. Prodr. **11**: 415. 1847.
Drejerella nemorosa (Swartz) Lindau in Urban, Symb. Antill. **2**: 223. 1900.

Jamaica. Parishes of TRELAWNY (*Powell 775*); MANCHESTER (*Purdie*); ST. ANN (*Alexander*); ST. ANDREW (*Harris 5650*; *Proctor 23334*); PORTLAND (*Bengry 4851*; *Yuncker 18422*), and ST. THOMAS (*Harris & Britton 10569*; *Proctor 26751*).

Justicia pectoralis Jacq. Enum. Pl. Carib. 11. 1760; Select. Stirp. Amer. 3. *t. 3.* 1763.

Dianthera foliis lanceolatis etc. Browne. Hist. Jam. 118. 1756.
Dianthera pectoralis (Jacq.) Murray in L. Syst. Veg. 164. 1784.
Stethoma pectoralis (Jacq.) Raf. Fl. Tellur. **4**: 61. 1838.
Rhytiglossa pectoralis (Jacq.) Nees in Mart. Fl. Bras. **9**: 128. 1847.
Ecbolium pectorale (Jacq.) Kuntze, Rev. Gen. Pl. **1**: 487. 1891.

Psacadocalymma pectorale (Jacq.) Bremek. in Verh. Kon. Nederl. Akad. Wet. Natuurk. II. **45**(2): 55. 1948.

Jamaica. Parishes of ST. JAMES (*Proctor 24720*) and ST. MARY (*Adams 12245*).

This species which occurs here and there throughout the West Indies and over Central America from Mexico to northern South America, was formerly cultivated in Jamaica as a medicinal plant.

CUBAN JUSTICIA SPECIES OF THE DREJERELLA GROUP

In Cuba, following Alain's treatment in Leon & Alain, *Flora de Cuba* **4**: 507, 508. 1957, there are five species of the *Drejerella* group distinguishable as follows:

1. Stem uniformly hairy all round. ..... *J. tomentosula.*
1. Stem unevenly hairy with two longitudinal bands of dense or long hairs separated by two much less hairy or almost glabrous spaces.
   2. Corolla 8–14 mm. long.
      3. Bracts obovate, narrowed into stalk. Corolla 8–12 mm. long. ..... *J. alainii.*
      3. Bracts rhomboid. Corolla 14 mm. long. ..... *J. maestrensis.*
   2. Corolla 18–25 mm. long.
      4. Leaf base cuneate. Lower lip of corolla much shorter than tube. ..... *J. mirabilioides.*
      4. Leaf base rounded. Lower lip of corolla about equalling tube. ..... *J. calcicola.*

Justicia alainii Stearn, nomen novum.

Adhatoda origanoides Nees in DC. Prodr. **11**: 407. 1847.
Justicia origanoides (Nees) Griseb. Pl. Cub. 197. 1866, non *J. origanoides* Vahl, 1805.
Drejerella origanoides (Nees) Lindau in Urban, Symb. Antill. 2: 225. 1900; Alain in Leon & Alain, Fl. Cuba **4**: 507. 1957.

An endemic Cuban species recorded from the provinces of Pinar del Rio, Habana, Las Villas, Camagüey, and Oriente and the Isla de Pinos, this was described under *Adhatoda* by Nees from a scrap of a specimen in W. J. Hooker's herbarium collected by his friend and American correspondent Dr. Benjamin D. Greene (1793–1862), first president of the Boston Society of Natural History and a great though unobtrusive benefactor of botany in New England. As noted by Urban (Symb. Antill. **3**: 53. 1902) there is no printed record of his visiting Cuba: "wann er in Cuba war, ist nicht bekannt." Neither Asa Gray in 1863 nor T. T. Bouvé in 1880 mentioned such a visit when outlining his career. The type specimen of *Adhatoda origanoides* Nees (K) is labeled "Havana." A letter of 28 May 1831 from Greene at New York to Hooker (Hooker correspondence 61 no. 122) elucidates this: "About three years ago since I passed a winter in *Havana* to avoid, on account of my wife's health, the severity of our winter. I there made a small collection of plants of the vicinity and

recollect on my return selecting some with the intention of sending them to you." He added that any West Indian plants he sent "must have been from Cuba," not Bermuda as Hooker supposed. Thus the Havana area is the type locality of *Adhatoda origanoides*. Unfortunately Nees's epithet *origanoides* cannot be retained under *Justicia* owing to the earlier *J. origanoides* Vahl, Enum. Pl. 1: 122. 1805, which is apparently synonymous with *Nelsonia canescens* (Lam.) Sprengel. It has accordingly been renamed in honor of Brother Alain (Dr. E. E. Liogier), formerly of the Colegio de la Salle, Habana, as a tribute to his work on the Cuban flora.

Justicia calcicola (Urban) Stearn, comb. nov.

Drejerella calcicola Urban, Symb. Antill. 9: 133. 1928.

Cuba. ORIENTE PROVINCE (*Ekman 7715*).

Justicia maestrensis (Urban) Stearn, comb. nov.

Drejerella maestrensis Urban, Symb. Antill. 9: 134. 1928; Alain in Leon & Alain, Fl. Cuba 4: 507. 1957.

Cuba. ORIENTE PROVINCE (*Ekman 8217*).

Justicia mirabilioides Lam. Tabl. Encycl. Illustr. Gen. 1: 39. 1791.

Beloperone lamarckiana Nees in DC. Prodr. 11: 415. 1847, nom. illegit.
Drejerella mirabilioides (Lam.) Lindau in Urban, Symb. Antill. 2: 222. 1900; Alain in Leon & Alain, Fl. Cuba 4: 508. 1957.

Cuba. (Oriente); Hispaniola, Puerto Rico, St. Thomas, St. Croix, Martinique (probable type-locality).

Justicia tomentulosa (Urban) Stearn, comb. nov.

Drejerella tomentulosa Urban, Symb. Antill. 9: 133. 1923; Leon & Alain, Fl. Cuba 4: 508. 1957.

Cuba. ORIENTE PROVINCE (*Ekman 3264, 7550*).

OPLONIA

Oplonia Raf. Fl. Tellur. 4: 64. 1838. FIGURE 5 A, B, C.

Anthacanthus Nees in DC. Prodr. 11: 460. 1847; Lindau in Urban, Symb. Antill. 2: 214. 1900.
Forsythiopsis Baker in Jour. Linn. Soc. London, Bot. 20: 218. 1883; Benoist in Humbert, Fl. Madag. 182: 106. 1967.

The names *Oplonia* and *Anthacanthus* both have as their type the same West Indian species, *Justicia spinosa* Jacq., and, although Rafinesque's name *Oplonia* has hitherto been ignored, the genus concerned is too small and unimportant to justify conservation of Nees's better known but later name *Anthacanthus*. The problems associated with its definition and geographical distribution have been discussed in "A survey of the tropical

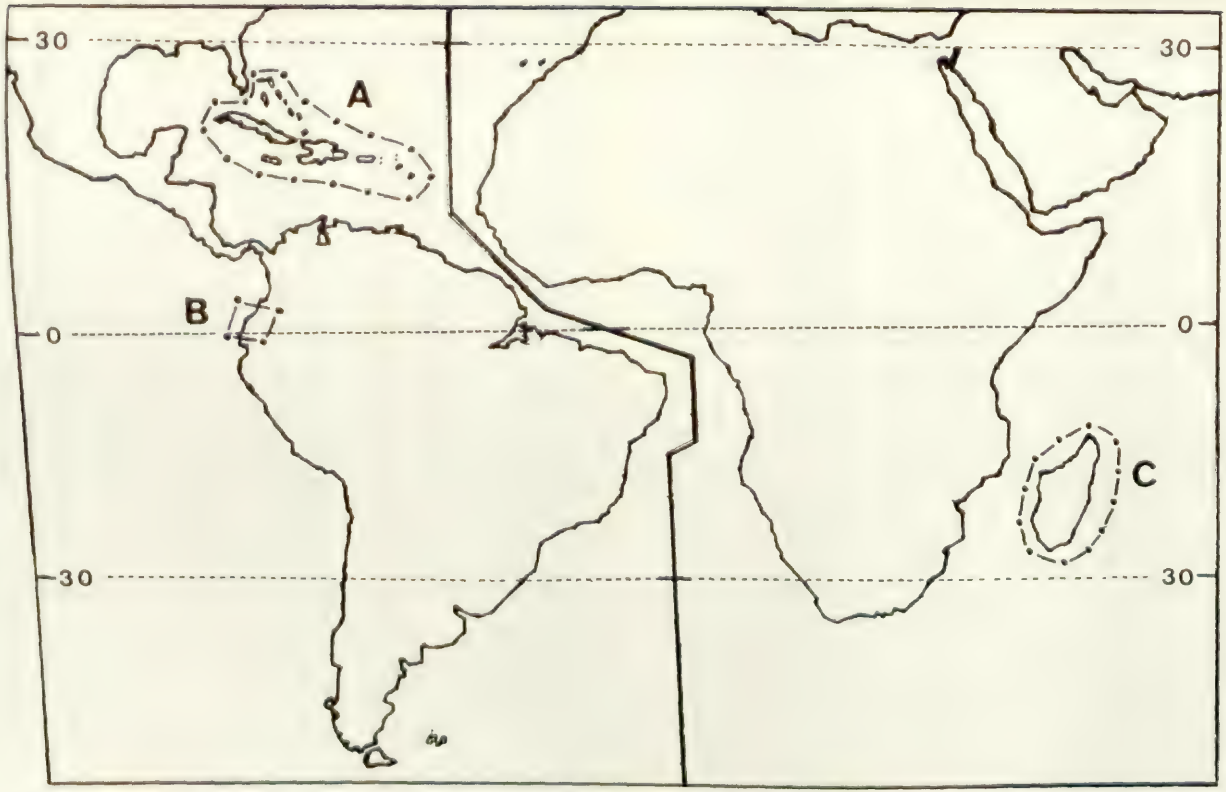

FIGURE 5. Map showing distribution of *Oplonia* and *Psilanthele* (Acanthaceae). A. West Indian species of *Oplonia* (*Anthacanthus*); B. South American species of *Oplonia* and *Psilanthele*; C. Madagascan species of Oplonia (*Forsythiopsis*).

genera *Oplonia* and *Psilanthele* (*Acanthaceae*)" in *Bull. Brit. Mus.* (*Nat. Hist.*), *Bot.* **4**: 259–323. 1971. *Forsythiopsis* was based on a Madagascan species, *F. baroni* Baker, later found to be conspecific with the earlier *Justicia vincoides* Lam., which Nees had included in *Anthacanthus*. Despite their wide geographical separation (cf. FIGURE 5), the American and Madagascan groups resemble each other so closely as to leave only the glabrous style of the one and the hairy style of the other for their morphological separation and their generic distinction. Both groups are heterostylous. It seems highly improbable that these manifold resemblances between them are the result of convergent evolution from different stocks rather than parallel or slightly divergent evolution from the same stock. If it is the latter, as I believe, then this advanced genus must have developed before the breakup of the Gondwanaland landmass in the Cretaceous period over 70 million years ago.

The taxa distinguished in the Jamaican flora are *O. acicularis* (*Justicia acicularis* Swartz, *Anthacanthus acicularis* (Swartz) Nees), *O. armata* with two varieties, var. *armata* (*J. armata* Swartz) and var. *pallidior* (*Psilanthele minor* Lindau), *O. jamaicensis* (*P. jamaicensis* Lindau) and *O. microphylla* (*Justicia microphylla* Lam.). The genus *Psilanthele* Lindau is restricted to Ecuador; Jamaican species included in it belong to *Oplonia*.

RUELLIA

Ruellia sceptrum-marianum (Vell.) Stearn, comb. nov.

Pedicularis sceptrum-marianum Vellozo, Fl. Flum. Descr. 269. 1825; Icones **6**: *t. 104*. 1831.

Ruellia acutangula Nees in Flora (Regensburg) **21** (Beibl. ii.): 61. 1838; Hooker f. in Curtis's Bot. Mag. **104**: *t. 6382*. 1878; Lindau in Urban, Symb. Antill. **2**: 196. 1900.

Arrhostoxylum acutangulum (Nees) Nees in Mart. Fl. Bras. **9**: 58. 1847; Nees in DC. Prodr. **11**: 210. 1847.

This is an ornamental large-leaved plant, with numerous large bright red flowers, native to Brazil, introduced into cultivation in England about 1876 and recorded from Jamaica by Lindau on the evidence of a specimen gathered by Hansen, which must have been cultivated; there is no evidence of its ever having become naturalized in Jamaica.

MAPS

The maps indicate the localities from which I have examined specimens. Thanks to the intensive botanical exploration of Jamaica during the past 30 years, particularly by G. R. Proctor of the Institute of Jamaica, enough material is now available for such maps to give a fairly reliable impression of the ranges of species within the island. Other maps will be found in the following papers.

STEARN, W. T. 1958. A key to West Indian mangroves. Kew Bull. **1958**: 33–37. [*Avicennia germinans.*]
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EXPLANATION OF PLATE

PLATE I

Forestiera. A–H. *F. rhamnifolia* var. *pilosa* Stearn: A, staminate inflorescence and underside of leaf; B, upper side of leaf; C, cluster of staminate flowers; D, single staminate flower; E, anther; F, fruiting branch; G, fruits; H, stigma. K, *F. segregata* (Jacq.) Krug & Urban: a, upper side of leaf, b, underside of leaf. [A–E from *Harris 9017*, F–H from *Harris 9056*, K from *Harris 9015*.] Plate drawn by Derrick Erasmus.

STEARN, FORESTIERA

THE LINACEAE IN THE SOUTHEASTERN UNITED STATES [1]

KENNETH R. ROBERTSON

LINACEAE S. F. Gray, Nat. Arr. Brit. Pl. 2: 639. 1821, "Lineae" [A. P. de Candolle, Théorie Élem. Bot. 214. 1813, "Linées"], nom. cons

(FLAX FAMILY)

Herbs [shrubs, trees or woody climbers] with simple and mostly alternate (rarely all opposite or whorled) leaves; stipules present or absent. Inflorescences various, cymose, racemose, corymbose, or paniculate [rarely solitary]. Flowers perfect, regular, 5[4]-merous; sepals and petals free or slightly connate at the base, the sepals quincuncially imbricate, the petals contorted in aestivation and often clawed; disc absent; stamens equal in number to the petals and alternate with them or twice as numerous and in two whorls, filaments connate at the base with nectar glands usually on the outside of the tube, staminodia sometimes present; ovary superior, syncarpous, 5[2–4]-carpellate, sometimes partially or completely subdivided into 10 [4–8] locules by the intrusion of false septa, ovules 2 per carpel, epitropous; styles as many as the carpels, mostly free or sometimes partly to completely united; stigmas distinct, capitate to filiform. Fruit a septicidal capsule [or drupe]; seeds often with a mucilaginous epidermis, embryo straight [or slightly curved]. (Linaceae sensu Hutchinson, 1967; Linoideae of Winkler, excluding Nectaropetaleae, and of Scholz.) TYPE GENUS: *Linum* L.

About 13 genera and 275–350 species of worldwide distribution, but with relatively few species in the Southern Hemisphere. Four genera are represented in North America: *Linum*, with about 41 (including 4 or 5

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants in this area, with additional information in brackets. References I have not seen are marked by an asterisk.

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introduced) species primarily in the Southwest and on the Atlantic and Gulf coastal plains; *Radiola* J. Hill (*Millegrana* Adanson), with *R. linoides* Roth introduced and established in Nova Scotia; *Hesperolinon* (Gray) Small, with 12 species largely confined to California; and the monotypic *Sclerolinon* C. M. Rogers, with *S. digynum* (Gray) C. M. Rogers ranging from Washington south to California. *Reinwardtia* Dumort. has been introduced into the West Indies from India. These genera, plus the Asian *Anisadenia* Wall. and *Tirpitzia* Hallier f., comprise the tribe Lineae (mostly herbs or subshrubs, stamens the same number as the petals, fruits capsular), which is generally of temperate regions. The tribe Hugonieae Planchon (trees, shrubs or woody climbers, stamens twice the number of the petals, fruits drupaceous) is mostly tropical and contains six genera, including the South American *Hebepetalum* Bentham and *Roucheria* Planchon. The family is evidently not indigenous to southern Central America, adjacent northern South America, and most of the West Indies.

Closely related to the Linaceae, or sometimes included within it, are the Humiriaceae, Ctenolophonaceae, Ixonanthaceae, and Erythroxylaceae, which share the simple leaves; regular flowers; diplostemonous androecium or stamens in only 1 whorl, rarely numerous, with the filaments basally united; nectiferous disc absent or small; and superior ovary. The Geraniaceae, Oxalidaceae, Malpighiaceae, Zygophyllaceae, and Polygalaceae are also sometimes considered to be related to the Linaceae. The Linaceae have recently been placed in the Linales (Cronquist), the Geraniales (Winkler, Scholz, Thorne, and Takhtajan), and the Malpighiales (Hutchinson, in his Lignosae). Hallier placed the Linaceae in his Guttales as a derivative of the Ochnaceae and considered it as the evolutionary center of origin for several lines, including the Passiflorales, Myrtales, Sapotales, Santalales, and some families of the Tubiflorae. Airy Shaw suggests that through *Anisadenia* the Linaceae are connected with the Plumbaginaceae, and Erdtman (1969) says that on palynological grounds these two families are close.

The floral anatomy and morphology of *Linum* and certain other genera have been the subject of numerous papers (cf. Sharsmith and Narayana). The stamens in the Lineae are monadelphous, with a cup from which the filaments arise. In some species and genera nonvascularized structures, usually called staminodia, alternate with the stamens. Sharsmith found in *Hesperolinon*, *Radiola*, and a few species of *Linum* that the petals arise from the cup in exactly the same position as the staminodia found in *Linum* and other genera. In other species of *Linum*, and in *Anisadenia* and *Reinwardtia*, the petals originate from the receptacle at the base or from the sides of the cup. In all cases the petals have but a single vascular strand, are only lightly attached to the cup or receptacle, and usually fall readily if disturbed. Collections of members of this family should be made early in the morning and be pressed immediately.

Reported chromosome numbers are *Hugonia* (3 spp.) $2n = 12, 24, 26$; *Radiola linoides*, $2n = 18$; *Reinwardtia trigyna*, $2n = 20, 22$; *Sclerolinon*

digynum, $2n = 16$; and *Linum*, $2n = 12, 16, 18, 20, 24, 26, 28, 30, 32, 34, 36, 52, 54, 60, 62, 68, 72, 84$.

Pollen grains of the Linaceae are diverse and of some taxonomic importance. The tribe Lineae has 3-, 4- or 6-colpate, pantocolpate, or pantoporate grains with a granular to baculate sexine, while the Hugonieae have mostly tricolporate grains with the sexine usually strongly baculate and often tegillate. The pollen of *Anisadenia pubescens* and *Reinwardtia indica* was reported as nonaperturate by Erdtman, but Saad describes both as pantoporate. Pollen morphology supports the removal of *Ctenolophon* and the Humirioideae from the Linaceae. Pollen of the woody members of the family is of a more advanced type than that of the herbaceous members. Saad and Erdtman have pointed out similarities between the Linaceae, especially *Hugonia*, and the *Plumbago* group of the Plumbaginaceae. Palynological similarities to the Geraniaceae and Oxalidaceae have also been noted.

Anatomical studies indicate that the Linaceae *sensu lato* is not a natural group and its division into several families is warranted. The Linaceae and Erythroxylaceae are considerably different anatomically, while the Linaceae and Humiriaceae have numerous similarities, with the wood of the latter family more primitive than the former and similar to *Ctenolophon*. Within the Linaceae, *Indorouchera* has the most primitive wood. There is no evidence from wood anatomy that the woody members of the family are derived from herbs.

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105; *Linum usitatissimum*, 258, 259; *L. hirsutum*, 294, 295; *L. alpinum*, 304, 305; *L. perenne*, 306, 307.]

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Tribe Lineae [Eulineae Planchon]

1. **Linum** Linnaeus, Sp. Pl. **1**: 277. 1753; Gen. Pl. ed. 5. 135. 1754.

Perennial or annual herbs [or shrubs], sometimes woody at the base, with one or several ± erect stems arising from a taproot or rootstock, usually unbranched below the inflorescence, stems mostly glabrous, infrequently scabrous [or pubescent], and often striate. Leaves simple and alternate, sometimes opposite below, infrequently all opposite [or whorled], ovate or obovate to linear, entire, denticulate or glandular toothed, mostly sessile with one midvein or several prominent parallel veins; stipules absent or paired and glandular. Inflorescences terminating the main stems, usually much branched and several to many flowered [rarely solitary], basically cymose but often appearing as scorpioid cymes, panicles, racemes or corymbs. Flowers yellow, blue [white or red]. Sepals 5, free or united at the base, lanceolate to ovate or obovate with acute to long attenuate apices, rarely obtuse, ± equal or the inner shorter than the outer, [glabrous or] all or only the inner glandular toothed, sometimes ciliate, with 1 or 3 prominent veins, persistent or infrequently deciduous, quincuncial. Petals 5, free [or connate by the claws], the lower adaxial surfaces pubescent or glabrous, inserted at the base of or on the staminal tube, fugacious, contorted, the claws or adaxial petal appendages small or almost absent. Stamens 5, alternate with the petals, basally united to form a cup around the ovary, nectar glands often on the outside of the cup; nonvascularized staminodia alternating with stamens or absent; anthers introrse, 2-locular at anthesis, opening lengthwise. Stigmas 5, distinct, capitate or clavate [to filiform]; styles 5, free or partly to almost completely united, homostylous [or heterostylous]; ovary superior, syncarpous, 5-carpellate but becoming ± 10-locular by the intrusion of incomplete to complete false septa, the true septa sometimes ciliate, ovules 2 in each carpel, pendulous,

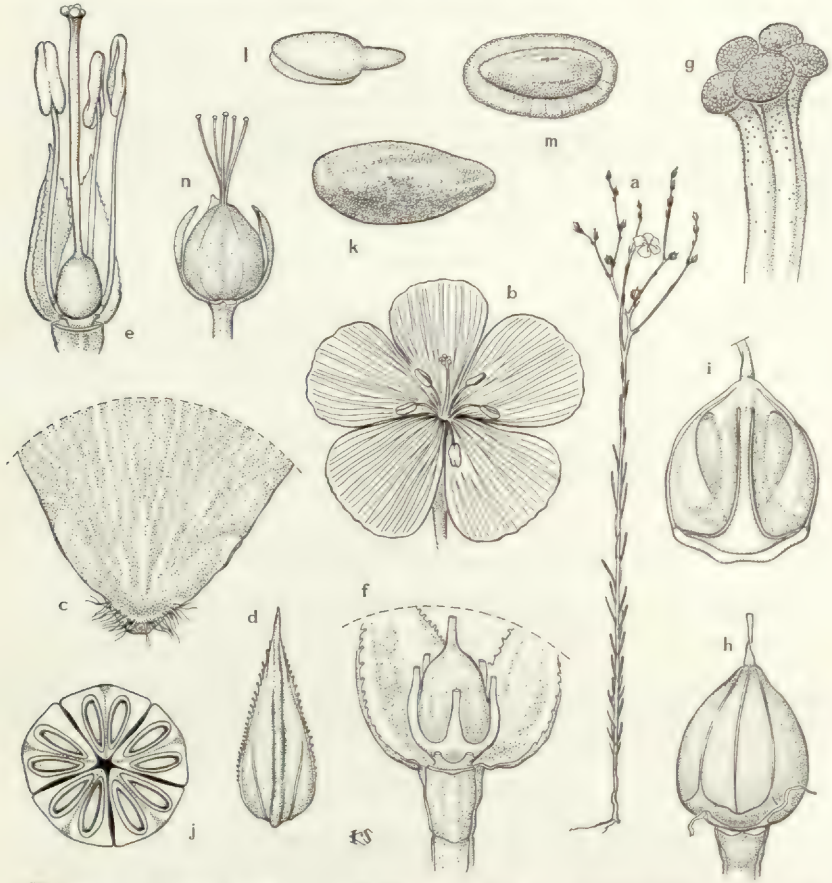

FIGURE 1. **Linum.** a–m, *L. Carteri* var. *Smallii*: a, plant with flower and immature capsules, × 1/4; b, flower, × 2; c, adaxial surface of petal base showing pubescent ligule with small abaxial pouches visible near margins, × 12; d, abaxial surface of outer sepal, × 6; e, flower (petals, three sepals and two stamens removed), × 5; f, flower (petals, three sepals and upper androecium and gynoecium parts removed) to show staminal cup and bases of filaments, two petal attachment points below, and nectar gland between petal attachment points, × 10; g, free capitate stigmas, upper part of style pubescent, × 20; h, capsule with persistent style and filaments (the sepals deciduous) — note basal cartilaginous plate, × 5; i, vertical section of capsule showing complete, partly cartilaginous and partly membranaceous false septa, two seeds visible through membranaceous part, × 6; j, semidiagrammatic cross section of immature capsule showing five 2-seeded segments which dehisce between the false septa (black), × 6; k, seed, surface scalariform, × 10; l, embryo, × 10; m, moistened seed surrounded by striated mucilage, × 6. n, *L. floridanum* var. *floridanum*: nearly mature capsule with persistent sepals (two removed) and distinct styles, a cartilaginous plate lacking, × 6.

axile, epitropous. Fruit a septicidal capsule, often beaked, dehiscing into 10 one-seeded or 5 two-seeded segments, the latter type with triangular

cartilaginous plates at the bases, usually dehiscing first between the false septa, rarely indehiscent; seeds sometimes retained within the capsule segments. Seeds compressed, smooth or slightly scalariform, mucilaginous when moistened; endosperm formation of the Helobial type, copious, scanty or absent in the mature seed; embryo straight. Embryo sac development of the Polygonum type, embryo development of the Solanad type. (Including *Cathartolinum* Reichenbach.) LECTOTYPE SPECIES: *Linum usitatissimum* L.; see J. K. SMALL, N. Am. Fl. 25: 67. 1907. (Ancient Latin name for flax and linen.) — FLAX.

A genus of 150–225 species widely distributed in temperate and subtropical regions, particularly in the Northern Hemisphere. Major centers of distribution are the Mediterranean region, the Balkan Mountains, Anatolia, the southwestern United States and Mexico, and the Coastal Plain province of the eastern United States. About 41 species occur in North America. In our area about fifteen species and seven varieties represent three major groups characterized by yellow, white, or blue flowers. The genus has not been examined on a world-wide basis since 1931, and the subgeneric classification is in need of re-evaluation, particularly the relationships between the North American species and those of South America, South Africa, and the Mediterranean region.

All species indigenous to our area belong to the "yellow-flowered" group, which is further characterized by small to medium-sized flowers, capitate stigmas, glands on all or the inner sepals, short pedicels, and all or at least the upper leaves alternate. These species are often placed in section CATHARTOLINUM (Reichenb.) Griseb., but are distinct and more closely related to the South American and Old World species referred to section LINASTRUM (Planchon) Reiche. These North American species, along with *Linum catharticum* L., were treated in the genus *Cathartolinum* Reichenb. by Small, who set up eight infrageneric units of undesignated rank, although some have considered them sections. Rogers and Harris have refined this scheme and recognize only five "species complexes" or "groups."

The *Linum Schiedeanum* complex, characterized by perennial habit, usual presence of stipular glands, persistent and glandular-toothed sepals, staminodia alternating with petals, essentially distinct styles, and capsules separating into ten one-seeded segments, includes fifteen species, with the greatest diversity in east-central Mexico. One member of the complex, *L. arenicola* (Small) Winkler, $2n = 36$, distinguished from other species in our area by its separate styles and prominent stipular glands, is endemic to the pine woodlands southwest of Miami, Florida, and on the western Florida Keys. It is closely related to *L. rupestre* (Gray) Engelm. ex Gray, $2n = 36$, of Texas, Mexico, and Guatemala, and *L. scabrellum* Planchon, $2n = 72$, of central Mexico. *Linum bahamense* Northrop, $2n = 68$, known from five islands in the Bahamas, is evidently more closely related to a group of central Mexican species than to *L. arenicola*.

The perennial *Linum virginianum* complex, comprising seven species and distinguished by the capsule separating into 10 one-seeded segments, absence of staminodia, persistent sepals with glandular teeth present only on the inner sepals or absent, distinct styles, and absence of stipular glands, is largely confined to the eastern half of the United States. *Linum intercursum* Bickn., $2n = 36$, with capsules ovoid and pointed at the apices, the septa ciliate, and the false septa clearly incomplete, occurs in the semishade of oak or pine woods along the Coastal Plain from Massachusetts south to the Carolinas and inland to Tennessee, northern Georgia, and Alabama; an isolated population is found in northwestern Indiana. Distinguished by subglobose capsules with rounded apices, nonciliate septa and inner sepal margins with conspicuous stalked glands, *L. medium* (Planchon) Britton var. *texanum* (Planchon) Fern. (*L. Curtissii* Small), $2n = 36$, is widespread in the East and also occurs in the Bahamas. The tautonymic variety, $2n = 72$, with thicker and wider leaves, is largely confined to the shores of the eastern Great Lakes. Particularly variable in southern Florida, this species needs further study. *Linum virginianum* L., $2n = 36$, has small subglobose capsules with umbilicate apices, sparsely ciliate septa, complete false septa, early dehiscing capsules which leave many specimens without fruit, and sepals glandless or with inconspicuous sessile glands. It is widespread in open woods of the northern and eastern United States, becoming infrequent in the southern Atlantic Coastal Plain. Closely related to the two preceding species, *L. striatum* Walt., $2n = 36$, is distinguished by its predominantly opposite leaves, ± elongate paniculate inflorescences, nonciliate septa, and glandless sepals. Ranging from eastern Texas and northern Florida to southeastern Missouri and eastern Massachusetts, with several collections from western Michigan, *L. striatum* is largely restricted to unglaciated regions. Occurring on the Coastal Plain from North Carolina to Louisiana and Florida, *L. floridanum* (Planchon) Trel. has mostly alternate leaves and capsules to 3 mm. long with nonciliate septa. Varietas *floridanum* (*L. macrosepalum* (Small) Winkler, *L. jamaicensis* (Small) Fawcett & Rendle), $2n = 36$, has broadly ovoid capsules suffused with purple, and var. *chrysocarpum* C. M. Rogers, $2n = 36$, has yellowish ovate capsules. Questionably distinct from the latter variety, known only from the type locality near Mobile, Alabama, and possibly now extinct, *L. macrocarpum* C. M. Rogers is distinguished from *L. floridanum* by the larger capsules (to 3.8 mm. long) with sparsely and inconspicuously ciliate septa. *Linum Westii* C. M. Rogers, $2n = 36$, known only from two locations in northern Florida and one in northern Georgia, has predominantly opposite leaves and subglobose capsules with abruptly pointed apices and nonciliate septa.

The *Linum sulcatum* "complex" includes only *L. sulcatum* Riddell, $2n = 30$, a common annual species of prairies and fields in the central and eastern United States. It resembles plants of the *L. Schiedeanum* complex in fruit shape and structure, persistent sepals and floral pigmentation, while the thick-walled polyporate pollen and basic chromosome number

of 15 are characteristic of the *L. rigidum* complex. Rogers (1969) suggests that although "it is perhaps unlikely that *L. sulcatum* is on a direct line of evolution connecting the *L. Schiedeanum* and *L. rigidum* complexes. . . . plants resembling *L. sulcatum* may have served as the link between the otherwise very distinct *L. Schiedeanum* and *L. rigidum* complexes." In our area, only *L. sulcatum* has basally united styles and all five sepals glandular-toothed and persistent. Certain collections from the Southeast with dark herbage and racemose inflorescences are sometimes segregated as var. *Harperi* (Small) C. M. Rogers (*L. Harperi* Small).

Typical members of the annual *L. rigidum* complex have capsules separating into five 2-seeded segments, no staminodia, sepals deciduous and at least the inner glandular-toothed, and styles united nearly to the summit. The group is composed of ten species, mostly of the southwestern United States and northern Mexico; two tetraploid populations are endemic to southern Florida, and at least three species occur in the extreme western part of our area. The Florida populations have been considered to be either varieties of *L. rigidum* Pursh, $2n = 30$, or a distinct species. Rogers (1968a), drawing on the biosystematic work of Mosquin & Hayley, treated the populations with puberulent or scabrous stems, stipular glands, petals 9–11 mm. long, and found only in the pinelands southwest of Miami as *L. Carteri* Small var. *Carteri*, $2n = 60$. The other populations in Dade, Collier, and Monroe counties with ± glabrous stems, stipular glands usually lacking, and petals 11.5–17 mm. long were identified as *L. Carteri* var. *Smallii* C. M. Rogers, $2n = 60$. *Linum Carteri* is most closely related to *L. rigidum* var. *Berlandieri* (Hooker) Torrey & Gray, $2n = 30$, with reddish pigment in the petals and thinner-walled capsules, occurring from southern Texas to eastern Colorado, northern Kansas, and western Arkansas and Louisiana. *Linum alatum* (Small) Winkler (*L. marginatum* Small), $2n = 30$, with unique glandular-toothed sepals with scarious margins, is largely confined to southern Texas and adjacent Tamaulipas, with one collection labeled "s.w. La." Another Texan species extending into our area in Louisiana is *L. imbricatum* (Raf.) Shinners (*L. multicaule* Hooker ex Torrey & Gray), $2n = 30$, with fringed glandless sepals and sparsely ciliate upper leaves.

The *Linum neo-mexicanum* complex is similar to the *L. Schiedeanum* complex, but staminodia are absent, and the base chromosome number is 13. None of the three species in this complex from the southwestern United States and northern Mexico approaches our area.

The "white-flowered" group, section CATHARTOLINUM (Reichenb.) Griseb., includes only *Linum catharticum* L., $2n = 16$. This delicate annual has numerous features in common with the "yellow-flowered" group, but the observations of Rogers and Sharsmith indicate that it is not closely related to the flaxes indigenous to North America. This widely distributed European species is established in Nova Scotia and Newfoundland with scattered locations west to Michigan and south to Pennsylvania. No other species in the region has small white flowers and opposite leaves. S. F. Gray

placed *L. catharticum* in his CHAMAELINUM, but the subgeneric category of this taxon is uncertain (cf. Brizicky, Taxon 18: 650. 1969); the name predates Grisebach's sectional combination.

The predominantly European "blue-flowered" group, section LINUM (*Eulinum* Griseb.), with medium to large flowers, linear to capitate stigmas, glandless sepals, long pedicels, all leaves alternate, and stipular glands absent, has only one or two species indigenous to the New World. Widespread in western North America, *L. Lewisii* Pursh, $2n = 18$, is sometimes cultivated in the East and has been reported from Cave Mountain, West Virginia (Allard). Plants with sepals less than 5 mm. long are sometimes segregated as *L. pratense* (J. B. S. Norton) Small, $2n = 18$. This variable complex has been considered conspecific with the European *L. perenne* L., $2n = 18, 36$, the only consistent difference between them being that *L. Lewisii*, like all the New World species, is homostylous, while *L. perenne* is heterostylous. The latter species is sometimes encountered as a garden escape. Other Old World species introduced to the eastern United States are the red- or pink-flowered *L. grandiflorum* Desf., $2n = 16$, a native of Algeria, and *L. usitatissimum* L. (*L. humile* Mill.), $2n = 30$, flax. One of the oldest cultivated plants, flax is grown both for the fibers from which linen is made and for the seeds which yield linseed oil.

Section CLIOCOCCA (Bab.) Planchon contains only the South American *L. selaginoides* Lam., and is perhaps best regarded as a distinct genus. The Old World sections, SYLLINUM Griseb. and DASYLINUM (Planchon) Juz., do not occur in North America.

Rogers (1969) suggests a monophyletic origin for the North American yellow-flowered flaxes with the *L. Schiedeanum* complex, which includes the most primitive members of the group, giving rise to three lines — the *L. virginianum* complex, the *L. neo-mexicanum* complex, and the *L. sulcatum* and *L. rigidum* complexes. East-central Mexico, the center of distribution for the *L. Schiedeanum* complex, is postulated as the region of establishment and diversification of the North American yellow-flowered group. Rogers points out that some South African species are very similar to *L. Schiedeanum*, and preliminary evidence (personal communication) indicates similarities between the South American species and certain Mexican and African species.

A chemotaxonomic study of floral pigments in North American yellow-flowered Linums (Giannasi & Rogers) further emphasized the distinctness of the *L. rigidum* complex, since it possesses the α-carotenoids leutin and its 5, 6-monoepoxide, while the other species complexes contain only the β-carotenoid violaxanthin. The distribution of the flavonoid pigments supports the presumed relationship between the *L. Schiedeanum* and *L. virginianum* complexes.

All species of *Linum* indigenous to North America are homostylous, while some Old World species are heterostylous. In some heterostylous species, such as *L. perenne*, both the filaments and styles are of different lengths while in others, such as *L. grandiflorum*, only the styles vary in length.

Charles Darwin first recognized that heterostyly is an out-breeding mechanism since the long-styled and short-styled forms are mostly self-sterile but cross-fertile; homostyled flowers are largely self-fertile. (See Baker's interesting paper for a misunderstanding between Darwin and Thomas Meehan, but also involving Asa Gray, about heterostyly and self-compatibility in *L. perenne* and *L. Lewisii*.)

The pollen morphology of *Linum* species is diverse. Aperture types are 3-, 4- or 6-colpate, pantocolpate and pantoporate. The tricolpate grains have been classified on the basis of aperture shape and size and the nature and texture of the nexine covering the colpi. The exine is thin, undulate or thick and bears surface processes that vary in size and shape. These processes may be monomorphic, dimorphic or polymorphic; in a few species the processes are united to form a tegillum which can bear suprategillar processes. The sexine shows a trend from a granular composition to the formation of distinct bacula. Ockendon found in the *L. perenne* group a correlation between aperture number and ploidy level, and between the morphology of the exine processes and the stylar condition of the flower. Yermanos & Gill (1967) report that in eight species the pollen was 3-colpate in diploids and 4-colpate in their autotetraploids. To some extent pollen morphological trends follow the subgeneric classification of *Linum*. The thick-walled polyporate pollen of the *L. rigidum* and *L. sulcatum* complexes is evidently the most specialized in the genus.

The North American and European species of *Linum* are well known cytologically, and definite base numbers have been determined in certain sections and species complexes. Polyploidy and aneuploidy have occurred in most groups. Base numbers are: *Linum Schiedeanum* complex, 18, 31, 34; *L. virginianum* complex, 18; *L. neo-mexicanum* complex, 13; *L. sulcatum* and *L. rigidum* complexes, 15; section CATHARTOLINUM, 8; section LINUM, 9, 15; section LINASTRUM (Old World species) 8, 9, 10; section SYLLINUM, 14; section DASYLINUM, 6, 8; and *Linum monogynum* from New Zealand, reported as having $2n = 84$. Numerous older undocumented and doubtful counts have been excluded. The hybridization studies of Gill, Gill & Yermanos, and Mosquin & Hayley indicate that chromosomal rearrangements, particularly translocations, have played a major role in the evolution of *Linum* species.

Hybridization in nature is evidently rare, but has been reported in the *Linum rigidum* and *L. virginianum* complexes. Artificial hybrids have been produced in the *L. rigidum* complex and in both the *L. perenne* and *L. usitatissimum* groups of section LINUM.[2] Autotetraploids of the *L. perenne* group ($2n = 36$) can hybridize with *L. usitatissimum* ($2n = 30$). Haploid plants of the latter species have also been produced. There are numerous reports of unsuccessful hybridization attempts involving mostly Old World species.

[2] D. J. Ockendon (personal communication) has obtained a hybrid between *L. Lewisii* and *L. Leonii*, a homostylous member of the European *L. perenne* group, which did not flower.

One *Linum* hybrid cross is often used as an example of the requirement that the hybrid embryo, endosperm, and seed coat be mutually compatible. In the *L. perenne* ♀ × *L. austriacum* ♂ cross, the hybrid embryo develops normally but cannot sprout through the seed coat. If removed, it grows into a vigorous and fertile F_1 hybrid. In the reciprocal cross, the embryo is inhibited and will not develop unless dissected from the seed and placed in a nutrient solution.

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A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR *

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31. **Caccinia** Savi, Cose Botaniche 1. *t. 1.* 1832.

Anisanthera Raf. Fl. Tellur. 3: 80. 1836.

TYPE SPECIES: *C. glauca* Savi.

Annual (?), biennial, or perennial hispid herbs; leaves alternate; inflorescence terminal; calyx usually divided for 2/3 to 3/4 of its length, never to the base, much enlarged in fruit; corolla tubular to hypocrateriform, tube narrow, long; faucal appendages well developed, large; stamens inserted adjacent to the bases of the faucal appendages, exserted at the apex of the corolla tube, unequal, 4 stamens very small, one very large; style filiform; nutlets 4, usually 1–2 developed, marginate or immarginate, ± compressed, smooth.

Species about 6, distributed in southwest and central Asia.

C. macranthera (Banks & Soland.) Brand, Pflanzenr. IV. 252(Heft 78): 90. 1921; Riedl in Rechinger, Fl. Iranica **48**: 227. 1967.

Borago macranthera Banks & Soland. in Russell, Nat. Hist. Aleppo, ed. 2. 2: 246. 1794.
Cynoglossum longiflorum Lehm. Asperif. 162. 1818.
Anisanthera ciliata Raf. Fl. Tellur. 11: 60. 1836.
Caccinia russellii Boiss. Diagn. Pl. Orient. Nov. I. 2(11): 134. 1849.

TYPE: Aleppo, *Russell s.n.* (BM).

Erect biennial (f. Boissier) to perennial herb. Stems fistulous, fleshy, angular, glabrous, simple or branched above, 20–80 cm. long. Leaves linear, linear-lanceolate, oblong or oblong-lanceolate, obtuse to acute, 7–23 cm. long, 6–40 mm. broad, covered on the upper surface and margins more densely than below with short, stiff, curved bristles, arising from large tuberculate bases, lower surface sometimes glabrous the bristles confined to the midrib. Inflorescence paniculate to thyrsoid-compound, terminal or axillary, short in flower, later elongated in fruit; bracts leaflike, narrower, and shorter. Pedicels erect, bearing few to many bristles, to 15 mm. long in flower, horizontal to subreflexed, to 25 mm. long in

* Concluded from volume 52, p. 522.

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fruit. Calyx to 8 mm. long in flower, divided for 3/4 of its length, lobes lanceolate, to oblong-lanceolate, acutish, 5–6 mm. long, to 2.5 mm. broad at base, margins of the upper half ciliate, those of the lower half setulose, midrib prominent with few scattered bristles, calyx enlarged to 35 mm. long in fruit, divided to nearly half its length, lobes triangular, to 17 mm. long and 12 mm. broad at base. Corolla tube 9–18 mm. long, lobes linear-oblong, spreading, 5–9 mm. long; faucal appendages puberulous, suborbicular, ± 1 mm. long. Stamens exserted, anthers unequal, one ± 5 mm. long, its filament 2 mm. long, the other 4 to 2 mm. long with filaments to 1 mm. long; filaments inserted at the throat of the corolla tube, adjacent to the bases of the faucal appendages. Nutlets grayish to grayish brown, ovoid to suborbicular, 5–11 mm. long, dorsally rugulose, irregularly tuberculate or minutely hirsute, margins dentate, teeth broadly triangular.

Distribution of species: Syria, Iraq, Iran, Armenia, Caucasus, Turkestan, Pamir Alaj, Afghanistan, West Pakistan.

Caccinia macranthera is very variable in its habit, leaf texture, and the position of its inflorescence. The following two varieties may be distinguished.

Var. macranthera.

Caccinia macranthera var. *eu-macranthera* Brand, Pflanzenr. IV. 252 (Heft 78): 90. 1921.

Biennial (teste Boissier). Stems ca. 30 cm. tall, branched near the base, branches divaricate. Leaves oblong-lanceolate, 8–11 cm. long, 10–15 mm. broad. Inflorescence large, paniculate, usually developed to the bases of stems.

Distribution of variety: As that of the species.

In the collections of this species from West Pakistan, I could not find any specimen of this variety. It is reported from east Afghanistan and may be expected in the western parts of our area.

Var. crassifolia (Vent.) Brand, Pflanzenr. IV. 252(Heft 78): 92. 1921: Riedl in Rechinger, Fl. Iranica 48: 228. 1967.

Borago crassifolia Vent. Descr. Pl. Jard. Cels. 100. *t. 100.* 1800.
Caccina glauca Savi, Cose Botaniche 1. *t. 1.* 1832; Ledeb. Fl. Rossica 3: 17. 1847; Boiss. Fl. Orient. 4: 277. 1875.
C. celsii Boiss. Diagn. Pl. Orient. Nov. I. 2(11): 132. 1849.
C. crassifolia (Vent.) C. Koch, Linnaea 22: 647. 1849; M. Pop. Fl. URSS 19: 686. 1953.
C. crassifolia (Vent.) C. Koch, f. *normalis* O. Kuntze, Acta Horti Petrop. 10: 212. 1887; Brand, Pflanzenr. IV. 252 (Heft 78): 92. 1921.
C. crassifolia (Vent.) C. Koch, f. *linearifolia* O. Kuntze, *ibid.*
C. crassifolia (Vent.) C. Koch, f. *persica*, f. *obtusifolia*, and var. *echinata* M. Pop. Acta Horti Bot. Univ. Jurjev. 12: 240, 241. 1911.

TYPE: Persia, inter Hamadan et Tehran, *Bruguière et Oliver, s.n.* (P).

ICON.: Savi, l. c. *t. 1.* 1832, under *C. glauca*; Vent. l. c. *t. 100.* 1800, under *Borago crassifolia.*

Perennial. Stems simple to branched, profusely leafy, 30–90 cm. tall. Leaves very variable, linear, lanceolate or oblong, 7–23 cm. long, 6–40 mm. broad. Inflorescence thyrsoid to paniculate-thyrsoid, terminal, rarely developed on the lower parts of the stems.

DISTRIBUTION OF VARIETY: as that of species, excluding the western parts of the area.

West Pakistan: GILGIT AGENCY: Northern Hindukush, *Giles s.n.* (K). QUETTA DIST.: Spin Karez, *Crookshank 152* (K); Quetta, *Peddie 318* (K), *Schmid 163* (K), Narai Kotal, *R. R. Stewart 3754* (K); Urak, *R. R. Stewart 28064* (K, RAW). Reported from: Baluchistan, *Stocks s.n.* (K?).

32. **Anchusa** L. Sp. Pl. 133. 1753; Gen. Pl. ed. 5. 64. 1754.

TYPE SPECIES: *A. officinalis* L. (lectotype species).

Perennial, biennial or annual crisp herbs. Calyx 5-fid to 5-partite, lobes more or less elongate in fruit. Corolla infundibuliform to hypocrateriform, tube straight to geniculate, lobes 5, regular to evidently zygomorphic; faucal appendages developed, usually large. Anthers inserted at the same distance from the corolla base on the corolla tube in the regular flowers, at different distances in zygomorphic flowers. Style filiform; stigma capitate to bilobed. Nutlets 4, erect to subhorizontal, areola large, basal to subventral, with fleshy thick rugulose collar.

Species 30–40, centering in the Mediterranean region, but extending through Europe, Africa, and western Asia.

KEY TO THE SPECIES

a. Biennial to perennial; corolla 13–15 mm. long, tube straight, limb regular. . . . . 1. *A. italica.*

a. Annual; corolla 6–7 mm. long, tube geniculate, limb irregular. . . 2. *A. ovata.*

1. **A. italica** Retz. Obs. Bot. 1: 12. 1779; Ledeb. Fl. Rossica 3: 119. 1847; Boiss. Fl. Orient. 4: 154. 1875; M. Pop. Fl. URSS 19: 306. 1953; Riedl in Rechinger, Fl. Iranica 48: 233. 1967.

A. azurea Mill. Gard. Dict. ed. 8: 9. 1768, *nomen confusum.*
A. paniculata Ait. Hort. Kew. 1: 172. 1789.

TYPE: not indicated.

ICON.: Bot. Mag. 48: *t. 2917.* 1820; Reichenb. Icon. Fl. Germ. 18: *t. 106.* MCCCVII. *fig. 5–8.* 1858.

Biennial to perennial herb. Stems usually solitary, branched in the upper

part, 30–60 cm. long, densely covered with white, spreading trichomes of unequal length, to 4 mm. long, arising from tuberculate bases. Basal leaves petiolate, lanceolate, entire, acute, including petioles to 35 cm. long, 6 cm. broad, covered on both surfaces, usually denser on the midrib and veins below, with trichomes more or less like those on the stem; cauline leaves sessile, reduced in size upwards. Inflorescence terminal or axillary, branched, short, scorpioid in flower, elongated in fruit; bracts linear to linear-lanceolate, to 20 mm. long, 2 mm. broad. Pedicels erect, hairy, 1–3 mm. long in flower, elongated to 10 mm. in fruit. Calyx divided to the base, lobes linear to linear-lanceolate, to 10 mm. long and 0.5–1.5 mm. broad in flower, not enlarged in fruit, densely covered with trichomes. Corolla rose-purple when young later turning to pure deep blue, 13–15 mm. long, limb spreading, 7–8 mm. in diameter; faucal appendages large, ciliate. Anthers included ± 2.2 mm. long; filaments ± 1.5 mm. long, inserted below the faucal appendages on the corolla tube. Nutlets erect, cylindrical, prominently reticulate-rugose, minutely tuberculate between the wrinkles, ca. 4 mm. long.

DISTRIBUTION: Central, southern, and southeastern Europe, North Africa, Turkey, Syria, Caucasus, Iran, Afghanistan, Turkestan, West Pakistan, and Kashmir.

West Pakistan: HAZARA DIST.: Dungagali, *Kazmi s.n.* (PES). QUETTA DIST.: Quetta, *Duthie 8686* (BM). RAWALPINDI DIST.: Murree, *R. R. Stewart s.n.* (RAW). **Kashmir:** Kotli, Hilal Khurd, *A. Rashid 26999* (BM).

Gusuleac (Bull. Fac. Stunte Cernaute 1: 273, 274. 1927) distinguishes three varieties of *Anchusa italica*, viz. var. *italica*, var. *macrocarpa* (Boiss. & Hohen.) Gusuleac, and var. *kurdica* Gusuleac. The specimens collected from West Pakistan and Kashmir belong to the typical variety. The other two varieties differ from the typical one in having trichomes of more or less equal length on the leaf surfaces with the areas between the bases of the trichomes densely pubescent. Var. *macrocarpa* is distributed in Turkish kurdistan, Caucasus, and Iran; whereas var. *kurdica* has its distribution in Cyprus, Syria, Palestine, Iran, and Iraq.

2. **A. ovata** Lehm. Asperif. 1: 222. 1818; Riedl in Rechinger, Flora Iranica **48**: 237. 1967.

Lycopsis orientalis L. Sp. Pl. 139. 1753.
L. micrantha Ledeb. in Pand. Beitr. 65. 1820.
L. taurica Stev. Bull. Soc. Nat. Moscou **40**: 337. 1857.
Anchusa orientalis (L.) Reichenb. Icon. Fl. Germ. **18**: 63. 1858. *non* Linn. 1753.
Lycopsis arvensis L. subsp. *orientalis* O. Kuntze, Acta Horti Petrop. **10**: 216. 1887.

TYPE: Habitat in Caria, *Lehmann, s.n.* (S?).

ICON.: Reichenb. Icon. **18**: *t. 109. fig. 14–16.* 1858, under *A. orientalis.*

Annual erect herb. Stems solitary to few, simple or branched, to 50 cm.

long, densely covered with spreading white trichomes of unequal length, to 2 mm. long, arising from tuberculate bases. Basal leaves petiolate, oblong-ovate, roundish at apex, entire to broadly and distantly dentate at margins, attenuated towards the base, including petioles to 12 cm. long and 2 mm. broad, covered on both surfaces with patent or subappressed trichomes with tuberculate bases; cauline leaves subsessile to sessile, sometimes decurrent, lanceolate to broadly ovate, obtuse to subacute, reduced in size upwards. Inflorescence foliate, terminal, short in flower, elongated in fruit. Pedicels slender, hairy, erect, very short in flower, later elongated to 12 mm. in fruit. Calyx divided to the base, lobes linear-lanceolate, acute, densely covered with stiff, long, spreading trichomes with tuberculate bases, 4–5 mm. long, 0.1–1 mm. broad in flower, elongated to 8(–10) mm., sometimes to 2.5 mm. broad at base in fruit. Corolla white to blue, infundibuliform, equalling or slightly exceeding the calyx, 5–6 mm. long, tube geniculate, limb shorter than the tube, to 2 mm. long, irregular, divided 1/2 to 2/3 of its length, lobes unequal; faucal appendages small, papillose. Anthers ovate, obtuse, ca. 0.8 mm. long; filaments very short, inserted 1.5–2 mm. above the corolla base. Nutlets transversely ovate, beaked, dorsally carinate, reticulate-rugose, minutely tuberculate between the wrinkles, areola subventral, large, margins thick, elevated, entire to slightly rugulose.

DISTRIBUTION: Bulgaria, Rumania, Turkey, Armenia, Caucasus, Transcaucasus, Iraq, Iran, Afghanistan, West Pakistan, Kashmir, northwestern India, northeast Africa.

West Pakistan: CHITRAL STATE: Arkari Gol, west of Tirich Mir, 2900 m., *Stainton 2610* (BM); Mastuj, Baroghil track, Shost, 3000 m., *Stainton 3034* (BM). GILGIT AGENCY: Baltistan, Indus River Valley, *Webster & Nasir 5888* (GH); Skardu, *R. R. Stewart 20426* (GH); Rupal to Gorikot, 2250–2350 m., *R. R. Stewart 18928* (GH); Gurez to Chorwan, Gilgit Road, 2250–2900 m., *R. R. Stewart 19627* (US); above Chorwan, Gilgit Road, 2300–2900 m., *R. R. Stewart 19696* (GH, US). KHYBER AGENCY: Khyber Pass, Afghanistan frontier, 600 m., *R. R. Stewart 9090* (GH). KURRAM AGENCY: Kurram valley, Serjal et Biaut Khel, *Aitchison 507, 569, 858* (GH). SWAT STATE: Mingora, *S. Ali 26098* (BM). Reported from: Swat State, inter Malakand et Barikot, 700 m., *Rechinger 30458* (W); North Waziristan, Khaisota, *J. L. Stewart s.n.* (?).

Kashmir: Ladak, Dras, 3000 m., *R. R. Stewart 10020A* (GH); Spitug, 3150 m., *Koelz 2678b* (GH, US); Pitug, *Koelz 6342* (GH, US); Pirpanjal Range, Nil Nag, 1350 m., *R. R. Stewart 23040* (GH); Kishanganga Valley, near Bhagtaur, 2200 m., *R. R. Stewart 17936* (GH); Srinagar, Nishat Bagh, *R. R. Stewart 23070a* (GH); Baramulla, 1500 m., *R. R. Stewart 13901B* (GH). Miscellaneous: Tibet occ., 12000–14000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH).

33. **Nonea** Medicus, Philos. Bot. 1: 31. 1789.

TYPE SPECIES: not indicated.

Annual, biennial or perennial hispid or villous herbs; leaves alternate. Inflorescence lax, racemose, elongate in fruit, foliate. Calyx 5-fid, short-

ly or for 1/2 its length, never divided to the base, enlarged in fruit, tube enclosing the nutlets; corolla campanulate-infundibuliform to subcylindric; faucal appendages distinct, fimbriate, or reduced to fimbriae or sometimes to pilosity only in throat, limb actinomorphic to slightly zygomorphic, lobes 5, imbricate in bud, short to long and spreading; stamens 5, included, anthers oblong, obtuse; ovary deeply 5-lobed, style filiform, stigma short or obscurely bilobed. Nutlets 4, erect with basal areola or more or less transversely ovate with subventral areola, usually rugose, areola of thick, elevated collar, entire to denticulate at margins.

Species about 25, chiefly Mediterranean, distributed in Europe, Asia, and North Africa.

Key to the Species

a. Corolla white.
  b. Corolla 8–9 mm. long; nutlets 4 mm. long, areola 1–1.5 mm. in diameter, collar 0.5–0.7 mm. high, denticulate at the margins. . . 3. *N. edgeworthii.*
  b. Corolla 6–7 mm. long; nutlets 2.5–3 mm. long, areola 1.5–2 mm. in diameter, collar 1.5–2 mm. high, not denticulate at the margins. . . . . 4. *N. turcomanica.*

a. Corolla red, violet, blue, or dark brown.
  c. Faucal appendages comparatively large, long lacerate, fimbria exserted. . . . . 2. *N. kandaharensis.*
  c. Faucal appendages very minute to lacking.
    d. Plants annual, corolla 7–12 mm. long, limb short, distinct to indistinct, regular to zygomorphic; areola 1–1.5 mm. in diameter. . . . . 1. *N. caspica.*
    d. Plants biennial to perennial; corolla 10–20 mm. long, limb long, usually equal half the length of the tube, never zygomorphic; areola 1.5–2 mm. in diameter. . . . . 5. *N. pulla.*

1. **N. caspica** (Willd.) G. Don, Gen. Syst. **4**: 336. 1838; Riedl in Rechinger, Fl. Iranica **48**: 250. 1967.

Onosma caspica Willd. Sp. Pl. **1**(2): 775. 1797.
Lycopsis caspica Lehm. Asperif. **2**: 256. 1818.
Anchusa picta M. Bieb. Fl. Taur.-Cauc. **1**: 137. 1808.
Lycopsis picta (M. Bieb.) Lehm. Asperif. **2**: 255. 1818.
Nonnea picta (M. Bieb.) Fisch. & C. A. Mey. Index Sem. Hort. Petrop. 43. 1835.
Nonnea diffusa Boiss. & Bhuse, Mem. Soc. Nat. Moscou **1860**: 152. 1860.
Nonnea nigericans "nigrescens" Auct. Fl. Orient. *non* DC. 1846.

Type: In arenosis versus Mare Caspicum, *Willdenow*.

Annual herb. Stems striate, usually many, sometimes solitary, usually ascendent or procumbent, rarely erect, simple, or branched, 5–30 cm. long, covered densely with minute, thin, crisped, spreading trichomes, to 0.5 mm. long, with or without minute tuberculate bases, intermixed densely or sparsely with stout, pungent, spreading trichomes, arising from prom-

inent tuberculate bases, 1–2 mm. long. Basal leaves petiolate, linear-lanceolate, oblong-lanceolate or oblong, entire to variously dentate, usually acute to rarely obtuse, including petioles 2–5(–6) cm. long, 3–10 mm. broad, covered densely with trichomes more or less like those on the stem, upper surface with more and longer trichomes than the lower surface. Inflorescence short in flower, later elongated. Pedicels pubescent, very short in flower, elongated to 4 mm. in fruit. Calyx divided for 1/3 to 1/2 its length, 5–7 mm. long in flower, lobes linear-lanceolate, acute, densely pubescent, enlarged and inflated in fruit, to 12 mm. long. Corolla red when young, turning to dark purple at maturity, 7–12 mm. long, limb distinct to indistinct, usually zygomorphic. Nutlets transversely ovate, 3–4 mm. long, dorsally slightly rugulose, covered with minute, slender trichomes, denser near the areola, areola longitudinally plicate, ridges radiating towards the body of the nutlet, 1–1.5 mm. in diameter, ca. 1.5 mm. high.

DISTRIBUTION OF SPECIES: European Russia, Caucasus, Iraq, Iran, Turkestan, Afghanistan, and West Pakistan.

The species is very variable in the form of cauline leaves and in the form and color of the corolla. The following subspecies may be distinguished.

KEY TO THE SUBSPECIES

a. Cauline leaves linear to linear-lanceolate, usually crisped-dentate.
  b. Corolla dark blue, cylindrical, hardly surpassing the calyx, limb not distinct. ..... 1a. subsp. *caspica*.
  b. Corolla red when young, later blue, infundibuliform, usually slightly zygomorphic, limb distinct. ..... 1b. subsp. *zygomorpha*.
a. Cauline leaves ovate-lanceolate to oblong, entire to flabellate-dentate.
  c. Corolla cylindrical, red to violet, limb short, indistinct, leaves entire to subdenticulate. ..... 1c. subsp. *melanocarpa*.
  c. Corolla infundibuliform, rosy red to violet, limb large, distinct, leaves flabellate-denticulate. ..... 1d. subsp. *schmidii*.

1a. Subsp. **caspica**.

Low growing, 5–10(–15) cm. tall, leaves linear-lanceolate, entire to ± lacerate, corolla short, subcylindric, limb minute, not evidently distinct.

DISTRIBUTION OF SUBSPECIES: As that of the species.

West Pakistan: CHITRAL STATE: Chitral Mastuj track, Buni, 1950 m., *Stainton 2465* (BM). LAHORE DIST.: Lahore, *Schlagintweit 10526* (US). QUETTA DIST.: Tak Pass, ca. 30 km. south of Quetta, 2100 m., *Kazmi 1286b* (PES), *Rechinger 28409* (W); between Bostan and Saran Tangi, 1700–1800 m., *Kazmi 1559b* (PES); *Rechinger 28187, 29188* (W); Spin Karez, 1800 m., *Kazmi 1586b* (PES); Quetta, *Duthie 8679* (K); Urak, Zarghun, 2350 m., *Santapau 6648* (GH); 33 to 34 miles from Quetta to Ziarat, *Kazmi 1578* (PES). RAWALPINDI DIST.: Agriculture Farm, Rawalpindi, *Y. Nasir 3356* (GH).

1b. Subsp. **melanocarpa** (Boiss.) H. Riedl, Oesterr. Bot. Zeitschr. 110: 527. 1963, in Rechinger, Fl. Iranica 48: 251. 1967.

Nonnea melanocarpa Boiss. Diagn. Pl. Orient. Nov. I. 2(11): 96. 1849.
Nonnea szowitsiana Stev. Bull. Soc. Nat. Moscou 24(1): 574. 1851.
Nonnea melanocarpa f. *macra* Boiss. ex Lipsky, Acta Horti Petrop. 26: 471. 1910.

TYPE: Circa Hierosolyman, *Boissier s.n.* (G).

Ascendent, suberect or rarely procumbent herb, 12–15(–20) cm. tall; leaves oblong to oblong-lanceolate, entire to lacerate, corolla small, subcampanulate, limb much shorter than the tube.

DISTRIBUTION OF SUBSPECIES: Palestine, Iraq, Iran, Caucasus, Afghanistan, Pamir Alaj, West Pakistan.

West Pakistan: QUETTA DIST.: Sariab, s. Quetta, 1700 m., *Rechinger 28815* (W).

1c. Subsp. **zygomorpha** H. Riedl, Oesterr. Bot. Zeitschr. 110: 527. 1963, in Rechinger, Fl. Iranica 48: 252. 1967.

TYPE: Ad confines Mesopotamiae et Arabiae borealis inter Meskene et Der-es Sor in tergo El Hilu inter vicos Sabcha et Tibne, *Handel-Mazzetti 548* (W).

Procumbent to ascendent herb, 10–20 cm. tall; leaves linear-lanceolate, usually deeply lacerate; corolla rosy red turning violet, 10–12 mm. long, limb distinct, nearly half as long as the tube, usually evidently zygomorphic.

DISTRIBUTION OF SUBSPECIES: Iraq, Iran, Afghanistan, West Pakistan.

West Pakistan: KALAT DIST.: Kalat, *R. R. Stewart 600A* (RAW). LAHORE DIST.: Lahore, April 1938, *H. Choudhuri s.n.* (GH).

1d. Subsp. **schmidii** H. Riedl, Oesterr. Bot. Zeitschr. 110: 529. 1963, in Rechinger, Fl. Iranica 48: 252. 1967.

TYPE: Persia: Prope Qazvin, 1200 m., *Schmid 5024* (G-holotype).

ICON.: Riedl l. c. *fig. 8.* 1963.

Plants 15–25 cm. tall; stems deflexed to ascendent; leaves oblong, lacerate; trichomes lax and thin as compared to the typical subspecies, corolla rosy-red when young, 10–12 mm. long, limb distinct, equalling half the length of the corolla tube or even shorter, never zygomorphic.

DISTRIBUTION OF SUBSPECIES: Afghanistan, Iran, Turkestan.

The subspecies *schmidii* has been reported from eastern Afghanistan and southern Iran and may be expected in West Pakistan.

2. **N. kandaharensis** Riedl in Køie & Rechinger, Biol. Skr. **13**(4): 226. 1963, in Rechinger, Fl. Iranica **48**: 248. 1967.

TYPE: Afghanistan: Kandahar, Shin Ghasi, zwischen Kandahar und Girischk am Hilmend, Blt. blau, 30. IV. 1935, *Kerstan 176* (HAL-holotype).

Annual low growing herb. Stems many, procumbent to ascendent, simple to branched, 5–15 cm. long, covered with long, spreading trichomes intermixed with short ones. Leaves 20–50 mm. long, 3–6 mm. broad; basal leaves petiolate, linear-lanceolate, acute to obtusish, attenuate towards the base; cauline leaves semiamplexicaul, covered on both surfaces with trichomes more or less similar to those on the stems. Inflorescence short and dense in flower, later elongated in fruit, foliate, these leaves similar to the upper cauline leaves 1 1/2–2 times longer than the calyces. Pedicels 2 mm. long. Calyx divided for half of its length, lobes lanceolate, 4–5 mm. long in flower, densely pubescent, elongated to 7–8 mm., inflated in fruit. Corolla purple-violet, blue when dried, cylindrical-campanulate, 6–8 mm. long, tube slightly dilated at throat, with long exserted fimbria, limb 1/3–1/2 the length of the tube, ± 3 mm. long. Nutlets transversely ovate, reticulate-rugose, 2–3 mm. long.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: Reported from (Riedl, *l. c.*): KALAT STATE: 40 km. N. Kalat versus Mastung, 2000 m., *Rechinger 28364* (W); QUETTA DIST.: Yaro prope Bostan, 1450 m., *Rechinger 28933* (W).

I was unable to examine the specimens of *N. kandaharensis* cited above. From the description it appears to be closely related to *N. caspica* (Willd.) G. Don, from which it is distinguished by having a much longer corolla limb, and the corolla throat bearing long exserted fimbria.

3. **N. edgeworthii** A. DC. in DC. Prodr. **10**: 30. 1846; Riedl in Rechinger, Fl. Iranica **48**: 249. 1967.

TYPE: India bor.-occid. ad Malwa, *Edgeworth s.n.* (K).

ICON.: Riedl, Oesterr. Bot. Zeitschr. **110**: 531, *fig. 9*. 1963.

Annual herb. Stems striate, usually many, sometimes solitary, ascendent to erect, simple to branched, to 35 cm. long, 5 mm. thick at base, branches to 15 cm. long, stem and branches puberulous to densely covered with minute, spreading or subappressed trichomes, to 0.5 mm. long, with or without tuberculate bases, intermixed sparsely, especially on the ridges, with stout, pungent, spreading, trichomes arising from prominent tuberculate bases. Basal leaves oblong-spathulate, obtuse, from the middle gradually narrowed towards the base into short petioles, petioles winged, dilated at base, including petioles to 8 cm. long, 10 mm. broad, densely covered on the upper surface, sparsely so on the lower surface with trichomes resembling those on the stem; middle cauline leaves ses-

sile, lanceolate, entire to irregularly and distantly dentate, obtuse to subacute, attenuate towards the base, to 10 cm. long and 15 mm. broad; upper cauline leaves shorter and narrower, margins bearing long trichomes, acute to acuminate, with slightly dilated bases. Inflorescence short in flower, elongated in fruit. Pedicels very short in flower, pubescent, recurved, elongated to 3–4 mm. in fruit. Calyx divided for nearly half of its length, 5–6 mm. long in flower, densely pubescent, elongated to 13 mm. in fruit, lobes lanceolate in flower, saccate, triangular, acute, to 5 mm. long in fruit. Corolla white, ± infundibuliform, 8–9 mm. long, limb hardly shorter than the tube, indistinctly zygomorphic, lobes short, rounded. Nutlets dark brown, transversely ovate, ± 4 mm. long, back convex, slightly rugose, glabrous, with white spots, sometimes sparsely pubescent near the areola, above the areola ventrally keeled, ridge continued on the dorsal surface and shifted to one side, acute at apex, areola 1–1.5 mm. in diameter, collar 0.5–0.7 mm. high, longitudinally plicate, plicae radiating towards the body of the nutlet, caruncle small.

DISTRIBUTION: West Pakistan, Kashmir, northwest India.

West Pakistan: ATTOCK DIST.: Dhok Pathan, *R. R. Stewart s.n.* (RAW). CHITRAL STATE: Chitral village, 1600 m., *Stainton 2207* (BM); Lutkor, 2600 m., *Bowes Lyon 798* (BM). JHELUM DIST.: Mt. Tilla, *Kabir 20430* (RAW). KURRAM AGENCY: Kurram Valley, *Afandi 1015a* (PES); Parachinar, *R. R. Stewart 28938* (RAW), *Harsukh 14437* (K). KHYBER AGENCY: Khyber Pass, *H. H. Johnston 57* (K). PESHAWAR DIST.: 7 miles from Peshawar, towards Khyber Pass, *Rodin 5295* (US). QUETTA DIST.: infra Bolan, 1500 m., *Rechinger 28784* (W); Quetta brewery, *N. Ali s.n.* (ICP). RAWALPINDI DIST.: Rawalpindi, 500 m., 30 March, 1938, *R. R. Stewart s.n.* (GH).

Kashmir: Reported from Jammu.

4. **N. turcomanica** M. Pop. Spiske Rast. Herb. Fl. URSS 12. No. 3575. 1953, Fl. URSS 19: 330. 1953; Riedl in Rechinger, Fl. Iranica 48: 249. 1967.

TYPE: Turcomania: In ditione Aschchabad, prope stationem experimentalem prope pagum Bagir, ad margine agrorum, 29 April 1950, *V. Nikitin 3575* (LE-holotype, A, W-isotypes).

Annual herb. Stems many, angular, erect to ascendent, slender, simple or branched, to 30 cm. long, covered densely with thin, spreading trichomes, 0.1–0.2 mm. long, intermixed sparsely with some slender, stiff, white trichomes with tuberculate bases. Basal leaves spathulate, entire, obtuse, attenuate at base, 4–5 mm. long, 5–8 mm. broad; middle cauline leaves narrow to broadly lanceolate; upper cauline leaves oblong-lanceolate to lanceolate, shorter, unequally denticulate on the lower half of their margins, both surfaces covered densely with soft, spreading trichomes to 0.2 mm. long, usually intermixed in the older leaves (more densely so on the upper surface and the margins) with long trichomes with tuberculate bases. Inflorescence of short or long racemes, bearing axillary flowers or

fruits. Pedicels very short in flower, pubescent, elongated to 3 mm. in fruit. Calyx in fruits saccate-ovate, densely covered with trichomes similar to those on the leaves, 6–8 mm. long, teeth acute, 1–2(–3) mm. long. Corolla white, narrowly subtubular, 6–7 mm. long, tube equalling the flowering calyx, ca. 4 mm. long, limb hardly dilated, narrowly campanulate, 2 mm. long, lobes small, obtuse, ca. 1 mm. long. Nutlets brown, 2.5–3 mm. long, incurved, subhorizontal, ventrally keeled above the areola, ridge continued through the acute apex on the dorsal side, shifting to one side, dorsally convex, slightly and sparsely rugulose, minutely puberulous all over the surface, areola large, 1.5–2 mm. in diameter, with a raised collar, ca. 1 mm. high, entire at the margins, caruncle small, mammiliform.

DISTRIBUTION: Iran, Afghanistan, Turkestan, West Pakistan.

West Pakistan: KURRAM AGENCY: Kurram Valley, Parachinar, 1500–1700 m., *Rechinger 30928* (W).

Nonea turcomanica is known from only one collection from Kurram Valley in West Pakistan. A close relative of this species cannot be suggested in our area, except that it is annual and has white flowers like *N. edgeworthii*. It differs from *N. edgeworthii* in leaf shape, length of corolla, and in its areolae. The nutlets are slightly rugose with large high collared areolae, entire at their margins. The description given above is based on the isotype in the Arnold Arboretum herbarium.

5. **N. pulla** (L.) DC. Fl. France, ed. 3. 626. 1805; Riedl in Rechinger, Fl. Iranica **48**: 247. 1967.

Lycopsis pulla L. Syst. Veg. ed. 10. 910. 1767.
Anchusa pulla (L.) M. Bieb. Fl. Taur.-Cauc. **1**: 125. 1808.

TYPE: "Hab. in Tartaria, Germania" Herb. No. 190.2 (LINN).

Perennial herb. Stems ascendent to erect, solitary to many, simple to branched, to 45 cm. long, densely covered with spreading to subappressed thin trichomes to 0.5 mm. long, with or without tuberculate bases, intermixed with long, pungent, white spreading trichomes, 1–2 mm. long, arising from prominent tuberculate bases. Basal leaves petiolate, lanceolate, 1–7 cm. long, 8–15 mm. broad, covered on both surfaces to some extent with trichomes similar to those on the stems; cauline leaves sessile, dilated to subamplexicaul at base; upper cauline leaves shorter and narrower, cauline leaves entire to distantly dentate, sometimes bearing longer trichomes, acute. Inflorescence few flowered, dense when young, later elongated. Pedicels short in flower, elongated to 5 mm. in fruit. Calyx 6–7 mm. long, hardly divided for half its length, lobes narrowly triangular in flower, much inflated, elongated 10–20 mm. in fruit. Corolla dark brown to dark purple, subcylindrical to campanulate, 10–20 mm. long, limb ca. half the length of the corolla tube. Nutlets dark brown transversely ovate, 3–4 mm. long, usually puberulous, dorsally slightly rugulose, areola 1.5–2 mm. in diameter with a thick, longitudinally

plicate collar, ridges radiating towards the body of the nutlet, caruncle large.

DISTRIBUTION OF THE SPECIES: Central and eastern Europe, Turkey, Caucasus, Iraq, Iran, Afghanistan (?), West Pakistan.

Nonea pulla is very variable in the form and indument of its cauline leaves, and in the length of the corolla. Riedl (*l. c.*) has classified these variations into four subspecies, viz. subsp. *pulla*, *macrantha*, *monticola*, and *rudbarensis*. Subspecies *pulla* is confined to Europe, subspecies *monticola* is spread over Turkey, Turkish Armenia, Iraq, and Kurdistan, whereas the other two subspecies are distributed in areas from Iraq to northwestern India. Subspecies *rudbarensis* occurs in West Pakistan.

Subsp. **rudbarensis** Rech. f. Ann. Naturh. Mus. Wien **55**: 17. 1947; Riedl in Rechinger, Fl. Iranica **48**: 248. 1967.

TYPE: North Persia: Gil: Rudbar, 200–500 m., *Bornmüller 7677* (w-holotype).

This subspecies is distinguished from the typical subspecies in having perennial rhizomes; dwarfed, often deflexed stems; narrowly lanceolate basal leaves with rigid trichomes, arising from tuberculate bases, intermixed on the inflorescence with stipitate glands; and the fruiting calyx with broadly triangular teeth.

DISTRIBUTION OF SUBSPECIES: Iraq-Kurdistan, Iran, West Pakistan, western India.

West Pakistan: ATTOCK DIST.: between Campbellpore and Grand Trunk Road, 300–400 m., *Kazmi 2733* (PES). LAHORE DIST.: Between Lahore and Shekhupura, ca. 400 m., 10 miles towards Shekhupura, *Kazmi 2905* (PES); Lahore. *Kazmi 2922* (PES); Muridke, ca. 400 m., *Kazmi 2955* (PES). RAWALPINDI DIST.: Rawalpindi, ca. 500 m., *R. R. Stewart 1510* (US). Miscellaneous: Punjab. Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH). Reported from: South Waziristan, Kaniguram, *J. L. Stewart, Blatter, Fernandez.*

The specimens cited above agree in the form of leaves, their indument, and in the length and color of the corolla with the specimens from Iran. In habit these are not dwarf but erect, to 50 cm. tall with thick branched stems, and leaves to 11 cm. long.

C. B. Clarke referred these plants to *Nonea pulla* sensu Lam. & DC. in Hook. f. Fl. Brit. India **4**: 169. 1883.

34. **Decalepidanthus** H. Riedl, Oesterr. Bot. Zeitschr. **110**: 608. 1963.

TYPE SPECIES: *D. sericophyllus* H. Riedl.

Very likely a perennial herb. Leaves dense, alternate. Inflorescence strongly contracted. Calyx divided to the base. Corolla tubular, included in the calyx, lobes longer than broad, acute; faucal appendages 10, inserted slightly above the corolla base. Stamens inserted on the middle of

the corolla tube, anthers small, ovate; filaments long, much exserted. Style slightly exserted from the corolla, glabrous, filiform, stigma deeply bilobed. Nutlets 4, free, slightly keeled dorsally, areola basal, fixed on the plane disciform gynobase.

One species endemic in West Pakistan.

D. sericophyllus H. Riedl, Oesterr. Bot. Zeitschr. **110**: 608. 1963.

TYPE: West Pakistan (NW-Frontier Province): Nathia Gali, N. of Rawalpindi, ca. 1800 m., 1907, *Sir Harold Deane s.n.* (K-holotype).

Basal parts of the plant not seen. Stems densely and softly pilose above, herbaceous, internodes to 1 cm. long; middle and cauline leaves sessile to subamplexicaul lanceolate to linear-lanceolate, acute, narrowed towards the base, 5–10 cm. long, 5–8 mm. broad, midrib sunken on the upper surface, raised and prominent below, secondary veins, usually several, indistinct, running towards the entire margin, the upper surface covered densely with soft, antrorsely appressed trichomes, the lower surface with ± pallid, silky trichomes; cauline leaves similar, smaller, and axillary, 2.5–3.5 cm. long, 2–4 mm. broad. Inflorescence terminal, geminate to ternate, rarely solitary in the axils of the upper cauline leaves, strongly contracted, bearing 5 to 7 flowers, elongate and lax in fruit; bracts lanceolate, 2–3 mm. long, ± 0.5 mm. broad. Pedicels indistinct to 1 mm. long in flower, elongated to 1.5(–2) mm. in fruit. Calyx divided to the base, lobes linear, appressed-pilose, 3.5–4 mm. long, to 0.5 mm. broad, not at all to slightly elongate in fruit. Corolla subtubular, slightly shorter than the calyx, 3.5 mm. long, lobes triangular, acute to acuminate, 1 mm. long, less than 1 mm. broad; faucal appendages 10, 5 alternating with the stamens, the other 5 alternating with the corolla lobes, ± 0.5 mm. long, about half as broad, inserted 0.2–0.3 mm. above the base of the corolla. Anthers broadly ovate, 0.7–0.8 mm. long; filaments slender, filiform, 3.5–4 mm. long, exserted, inserted on the middle of the corolla tube. Style filiform, 4.5–5 mm. long, stigma deeply bilobed. Nutlets (only very immature ones seen) dorsally slightly carinate, smooth, attached basally to the plane gynobase.

DISTRIBUTION: West Pakistan.

West Pakistan: HAZARA DIST.: Nathiagali, *Deane s.n.* (K).

I did not see the type or any other authentic material of this species, on which the genus is based. The description given here is according to Riedl (*l. c.*).

35. **Gastrocotyle** (Bunge) Benth. & Hook. Gen. Pl. **2**: 853. 1876.

Anchusa L. Sect. 5. *Gastrocotyle* Bunge, Mém. Acad. Sci. St. Pétersb. Sav. Étr. **7**: 405. 1851.

TYPE SPECIES: *G. hispida* (Forssk.) C. B. Clarke.

Annual or perennial (?) herbs; calyx divided to the base; corolla subtubular, faucal appendages small; stamens 5, included, anthers ovate, obtuse; ovary 4-lobed, style short, subcapitate. Nutlets ovoid, erect, incurved, reticulate-rugose, areola ventral with elevated, dentate margins affixed to the carpophore which is half the length of the nutlets.

Species two, distributed from North Africa and Asia Minor to West Pakistan and India.

G. hispida (Forssk.) C. B. Clarke in Hook. f. Flora Brit. India **4**: 168. 1883; Riedl in Rechinger, Fl. Iranica **48**: 254. 1967.

Anchusa hispida Forssk. Fl. Aegypt.-Arab. 40. 1775; DC. Prodr. **10**: 50. 1846; Boiss. Fl. Orient. **4**: 158. 1875.

TYPE: In desertis Kahirinis, *Forsskål s.n.* (C).

Annual herb. Stems many, fleshy, prostrate to suberect, to 40 cm. long, much branched, covered densely with spreading, thick trichomes of various lengths to 1 mm., arising from prominent tuberculate bases. Basal leaves very variable, petiolate, oblong, (including petioles) to 15 cm. long and 10 mm. broad, covered on both surfaces with spreading, stout, white trichomes of various lengths to 2 mm. long, with large tuberculate bases, sometimes falling off in age; lower cauline leaves short petiolate, undulate at margins; upper cauline leaves sessile, shorter and narrower. Flowers axillary, solitary, or in small axillary racemes. Pedicels very short, hardly elongated in fruit. Calyx divided to the base, lobes obtuse, densely covered with thick trichomes, ca. 2 mm. long, hardly enlarged in fruit. Corolla pale purple to light blue, subtubular, ± 3 mm. long, tube equalling the calyx, limb 1 mm. long, divided nearly to the base, lobes ovate, spreading; faucal appendages villous. Nutlets brown, ovate, dorsally strongly convex, rugulose, minutely tuberculate, areola ventral, large, with thick, elevated, dentate collar.

DISTRIBUTION: North Africa, Sinai, Arabia, Syria, Iraq, Iran, Trans-Caspian to Soongaria, Afghanistan, West Pakistan, Kashmir, western India.

West Pakistan: GILGIT AGENCY: Baltistan, Skardu, 2300 m., *Webster & Nasir 5767* (GH). LAHORE DIST.: Lahore, April, 1936, without collector's name *s.n.* (GH). PESHAWAR DIST.: Peshawar, *Nath 15459* (GH). RAWALPINDI DIST.: near Agriculture Farm, Rawalpindi, *Nasir 3357* (BM). Miscellaneous: Punjab, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH).

Kashmir: Reported from Lower Jhelum Valley; Mirpur, plains to ca. 1700 m. (R. R. Stewart, Check list of the flowering plants of West Pakistan and Kashmir — unpublished).

36. **Myosotis** L. Sp. Pl. 131. 1753; Gen. Pl. ed. 5. 63. 1754

TYPE SPECIES: *M. scorpioides* L.

Annual, biennial or perennial, pubescent herbs. Leaves alternate; in-

florescence scorpioid when young, later racemose, ebracteate; flowers usually white, blue, or purple; calyx lobed to deeply divided, not at all to slightly enlarged in fruit; corolla usually hypocrateriform, rarely campanulate or infundibuliform, lobes 5, convolute in bud, obtuse, spreading; faucal appendages 5, distinct; stamens 5, included, anthers ovate, obtuse; ovary deeply 4-lobed, style filiform, stigma small, disciform, mucronate; nutlets 4, usually ovoid, rarely subtrigonal-pyramidal, usually compressed, glabrous, smooth, shining, areola small, gynobase usually flat, sometimes slightly elevated.

A cosmopolitan genus of about 60 species, with two important centers of distribution, Europe and New Zealand.

KEY TO THE SPECIES

a. Calyx sparsely covered with short, rigid, appressed trichomes of equal length, never uncinate at apex.
  b. Style much shorter than the calyx. . . . . 1. *M. caespitosa.*
  b. Style equalling the calyx. . . . . 2. *M. palustris.*
a. Calyx densely covered with trichomes of various lengths, usually those at the base of the calyx spreading, partly uncinate at apex.
  c. Plants annual, pedicels much shorter than the fruiting calyx.
    d. Calyx persistent, erect, appressed to the inflorescence axis; connate part of the calyx covered with spreading, curved to uncinate trichomes, sometimes intermixed with straight ones, trichomes on the lobes appressed. . . . . 3. *M. stricta.*
    d. Calyx deciduous, spreading to deflexed, connate part of the calyx covered with uncinate trichomes, intermixed with numerous retrorsely appressed ones, trichomes on the lobes spreading. . . . . 4. *M. refracta.*
  c. Plants biennial to perennial, pedicels longer or equalling the fruiting calyx.
    e. Nutlets roundish to obtuse at apex, margined only on the upper half, calyx rounded or cuneate at the base.
      f. Corolla white to indistinctly bluish, calyx broadly rounded at the base, nutlets broadly margined at the top, not keeled ventrally near the apex. . . . . 6. *M. albicans.*
      f. Corolla blue to bluish purple, calyx narrow, attenuate towards the pedicels, nutlets narrowly margined at the top, distinctly or indistinctly keeled ventrally near the apex. . . . . 5. *M. alpestris.*
    e. Nutlets acute at apex, margined all around, margins narrow, calyx always rounded at base.
      g. Plants fleshy, less branched, calyx wide open in fruit, corolla 5–6 mm. in diameter. . . . . 7. *M. silvatica.*
      g. Plants not fleshy, much branched, calyx lobes more or less incurved in fruit; corolla to 2.5 mm. in diameter. . . . 8. *M. arvensis.*

1. **M. caespitosa** Schultz, Prodr. Fl. Stargard, Suppl. 1: 11. 1819; DC. Prodr. 10: 105. 1846; Ledeb. Fl. Rossica 3: 144. 1847; Boiss. Fl. Orient. 4: 235. 1875; C. B. Clarke in Hook. f. Fl. Brit. India 4:

173. 1883; M. Pop. Fl. URSS 19: 366. 1953; Riedl in Rechinger, Fl. Iranica 48: 257. 1967.

M. scorpioides L. subsp. *caespitosa* (Schultz) Hermann in Hegi. Illustr. Fl. Mitt.-Eur. 5(3): 2164. 1927.

M. lingulata Lehm. Asperif. 110. 1818, *nomen nudum*.

M. uliginosa Schrad. in Mert. & Koch, Röhlings Deutschl. Fl. 2: 42. 1826; ex A. DC. in DC. Prodr. 10: 105. 1846, *nomen nudum*.

TYPE: Ad pagum Ballin hinter dem Hofgarten, et prope Neobrandenburg am kleinen Ihlpol, *C. F. Schultz s.n.* (B).

ICON.: Reichenb. Icon. Fl. Germ. 18: *t. 120, fig. 1–5*. 1856, under *M. lingulata*.

Perennial, erect to suberect herb with fibrous, adventitious roots. Stems fleshy, usually solitary to sometimes many, simple to branched, to 60 cm. long, branches slender, ascending to spreading, sparsely covered with white, antrorsely appressed trichomes to 0.5 mm. long, with minute tuberculate bases. Basal leaves oblong-ovate, entire, rounded to subobtuse, slightly attenuate towards broad base, 2–3 cm. long, 5–8 mm. broad, upper surface uniformly and sparsely covered with trichomes like those on the stem, lower surface glabrous or with some scattered trichomes; lower cauline leaves oblong-obovate to oblong-lanceolate, obtuse, usually broadest at the middle of the upper half, gradually narrowed towards the base, 3–6 cm. long, 5–10 mm. broad; upper cauline leaves oblong-ovate to ovate, obtuse to subacute, gradually reduced upwards. Inflorescence very short, scorpioid in flower, later elongated, usually curved, bearing fruiting calyces ca. 10 mm. distant, to 30 cm. long in fruit, ebracteate. Pedicels very short in flower, slender, appressed hispid, ± horizontal, always longer than the calyx, to 10 mm. long in fruit. Calyx divided ± one half its length, cuneate at base, 1.5–2 mm. long in flower, to 3.5–4 mm. in fruit, lobes short, erect, obtuse to subacute, sparsely covered with appressed trichomes, 0.2–0.3 mm. long. Corolla blue, 2–3 mm. long, tube equalling the calyx, slightly narrowed at the throat, limb 1.5 mm. long, 3–4 mm. in diameter, divided for nearly half its length, lobes ovate, spreading. Style much shorter than the calyx. Nutlets broadly ovate, mature ones dark brown, shining, smooth, narrowly margined, with rounded apex, 1–1.5 mm. long, ca. 1 mm. broad, areola minute, 0.5 mm. broad.

DISTRIBUTION: Temperate and subtropical regions of Europe, Asia, North America, and North Africa.

West Pakistan: GILGIT AGENCY: Baltistan, Skardu, 2400 m., *R. R. Stewart 20419* (GH); Skardu, along irrigation canal near Indus River, 2250 m., *Webster & Nasir 5778* (GH); Kangan to Wangat, 1650 m., *R. R. & I. D. Stewart 18073* (GH). HAZARA DIST.: Siran Valley, between Dadar and Shahid Pani, *Kazmi s.n.* (PES). SWAT STATE: Kalam, ca. 2300 m., *Kazmi 152b* (PES), 19. 7. 1963, *R. R. Stewart s.n.* (BM), *A. Rahman 6* (BM); along trail by Swat River, near Kalam, 25 miles above Bahrain, 1800–2100 m., *Rodin 5620* (US).

Kashmir: Pahlgam, 2100 m., *R. R. Stewart 7903a, 8002, 12548* (GH), *21472*

(GH, US); vicinity of Pahlgam, on east Liddar Valley, 27 road-miles north of Islamabad, 2400–2900 m., *Dickason 79* (MICH); Srinagar, Aug. 1922, *Barbous s.n.* (BM); Shalimar Bagh (Srinagar), *Dickason 78* (MICH); Ganderbal, 1650 m., *R. R. Stewart 7161* (K); Shapiyon, 2400 m., July 9, 1896, *C. B. Clarke 28600a* (BM); Tangmarg, 1800 m., *Polunin 380* (BM); Anchar Lake, 1560 m., *Ludlow & Sherriff 8074* (BM, GH). Miscellaneous: without locality, Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM, K).

2. **M. palustris** (L.) Nath. Fl. Monspel. 11. 1756; M. Pop. Fl. URSS **19**: 363. 1953; Riedl in Rechinger, Fl. Iranica **48**: 257. 1967.

M. scorpioides L. var. *palustris* L. Sp. Pl. 131. 1753.

TYPE: Habitat in Europae aquosis scaturiginosis.

ICON.: Hegi, Fl. Mitt.-Eur. **5**(3): *t. 221. fig. 4.* 1927 under *M. scorpioides* subsp. *palustris*; Reichenb. Icon. Fl. Germ. **18**: *t. 109.* 1856.

This species is very similar to *Myosotis caespitosa* from which it is distinguished by having the style equal to the calyx, calyx divided only 1/3 of its length, 3 mm. long in flower, elongated to 4–5 mm. in fruit, calyx lobes more or less triangular, corolla limb 5–8 mm. in diameter.

DISTRIBUTION: Temperate regions of Eurasia and North America.

West Pakistan: SWAT STATE: inter Madyan et Kolalai, *Rechinger 30684* (W); Kalam, 2200 m., *Rechinger 19399* (W); Utror, 2500 m., *Rechinger 19580* (W).

I was unable to see the Rechinger collections cited above. All the specimens from our area examined by me have the styles always shorter than the calyx, the calyces not exceeding 4 mm. in length, and divided for nearly half their length. This material is of *Myosotis caespitosa*.

3. **M. stricta** Link in Roem. & Schultes, Syst. Veg. **4**: 104. 1819; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 174. 1883; Riedl in Rechinger, Fl. Iranica **48**: 264. 1967.

M. micrantha auct. plur., non Pall. ex Lehm. Neue Schr. Naturf. Ges. Halle 3(2): 24. 1817.

M. arenaria Schrad. in C. F. Schultz, Prodr. Fl. Stargard. Suppl. **1**: 12. 1819.

TYPE: "In arvis," without citation of collector's name (?).

Annual herb. Stems usually many, erect to ascendent, profusely branched, to 40 cm. long, 2–3 mm. thick at base, covered densely with white, crisped, spreading, unequal trichomes to 5 mm. long, thicker and longer trichomes usually arising from tuberculate bases. Basal leaves oblong to oblong-spathulate, entire, obtuse to rounded, attenuated toward the broad or narrow base, to 4 cm. long, 12 mm. broad, covered on both surfaces with spreading trichomes to 1 mm. long, usually tuberculate at base; upper cauline leaves few, sessile, ovate-lanceolate, obtuse, covered densely on the upper surface with subappressed, thinner and longer tri-

chomes (usually lacking basal tubercles), less densely on the lower surface with shorter, spreading tuberculate trichomes. Inflorescence short in flower, elongated to 20 cm. in fruit, bearing fruits 3–5 mm. apart, ebracteate. Pedicels hardly conspicuous in flower, hairy, suberect, usually parallel to the inflorescence axis, rarely subhorizontal, never recurved or reflexed, always much shorter than the calyx, 1–2.5 mm. long in fruit. Calyx rounded at base, divided to nearly half its length, ± 2 mm. long in flower, base slightly tapering towards the pedicel, densely covered with thin long trichomes, antrorsely appressed at least at the lobes, intermixed with stout, thick, curved to uncinate trichomes usually on the connate part, rarely above, elongated to 3–4 mm. in fruit. Corolla light blue, tubular-campanulate, obviously longer than the calyx, limb short, 2–3 mm. in diameter, lobes spreading. Nutlets dark brown, ovate, subacute, rounded at base, smooth, shining, 1.3–1.5 mm. long, 0.8–0.9 mm. broad, areola minute.

DISTRIBUTION: North Africa, Europe, Turkey, Syria, Iran, Afghanistan, West Pakistan, Kashmir, northwest India.

Kashmir: Muzzaffarabad, Handu Hills, ca. 2100 m., *Kazmi 225b* (PES); Tangmarg, 2200 m., *R. R. Stewart 12547* (GH). Miscellaneous: Himal. bor. occ. Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (K); without locality, Herb. Late East India Co., *Falconer s.n.* (GH).

Myosotis stricta may be expected in West Pakistan.

4. **M. refracta** Boiss. Voy. Bot. Espagne **2**: 433. 1839; Riedl in Rechinger, Fl. Iranica **48**: 264. 1967.

TYPE: In monte Sierra de la Nieve en el Pilar de Tolox, *Prolongo s.n.* (G).

Annual decumbent to erect herb. Stems usually solitary, sometimes few, much branched near the base, to 25 cm. long and 1.5 mm. thick at base, densely covered with white, ± soft, retrorsely suberect trichomes on the lower part, with spreading ones to 0.7 mm. long on the upper part, usually lacking basal tubercles. Basal leaves ovate to oblong-ovate, entire, obtuse to roundish, narrowed at base to a short petiole, (including petioles) 1–2 cm. long, densely covered on the upper surface, sparsely so on the lower surface with white, crisped trichomes to 0.5 mm. long, arising from tuberculate bases; cauline leaves sessile, oblong-ovate, obtuse to subacute, gradually reduced in size upwards. Inflorescence terminal, simple, short in flower, later elongated to 12 cm., with fruits 3–6 mm. apart, ebracteate. Pedicels scarcely 0.5 mm. long in flower, elongated to 1.5 mm. in fruit, horizontal, slightly recurved to strongly reflexed, often deciduous. Calyx pubescent, divided for 1/2 to 3/4 its length, 1–1.5 mm. long in flower, enlarged to 4 mm. in fruit, including the lanceolate, acute, erect lobes (2 mm. long), connate part 1.5–2 mm. long, usually narrowed towards the base, covered all over (more densely so on the basal

area) with thick, sometimes uncinate or recurved stout trichomes, intermixed with ± straight, shorter, thinner ones. Corolla blue, tubular-campanulate, 1.5–2 mm. long, tube ± equalling the calyx, lobes ovate to roundish, suberect to patent, ± 0.5 mm. long, nutlets ovate to ovate-oblong, glabrous, shining, 1–2 mm. long, areola small.

DISTRIBUTION OF SPECIES: Southern Europe, Turkey, Iraq, Iran, Afghanistan, Turkestan, Pamir Alaj, Tien Shan, West Pakistan, Kashmir, northwest India.

4a. Subsp. **refracta.**

Calyces strongly reflexed in fruit, connate part somewhat longer than the calyx lobes. Nutlets ca. twice as long as broad, broadest at the middle, gradually narrowed at both ends, 1.5–2 mm. long.

DISTRIBUTION OF SUBSP.: Southern Europe, Turkey, Iraq, Iran.

4b. Subsp. **chitralica** Kazmi, subsp. nov.

TYPE: West Pakistan: Chitral, Chitral-Mastuj tract, Suni, 6500 ft., on stony ground, flowers blue, 16 May, 1958, *J. D. A. Stainton 2458* (BM-holotype).

Calyces subhorizontales, horizontales vel subreflexi, raro perreflexi; tubus calycis plus minusve lobos calycis aequans. Nuculae 1.5 longiores quam latae, supra basim rotundatam latissimae, apex obtusus, 1–1.5 mm. longae, 0.7–0.9 mm. latae.

DISTRIBUTION OF SUBSP.: Afghanistan, West Pakistan, Kashmir, northwest India, Turkestan, Pamir Alaj, Tien Shan (?).

West Pakistan: CHITRAL STATE: Chitral-Mastuj tract, Suni, 1950 m., *Stainton 2458* (BM).
Kashmir: Srinagar, 1700 m., *R. R. Stewart 11089* (GH).

Myosotis refracta is closely related to *M. stricta* in its annual habit, its stems much branched at the base, and pedicels shorter than the calyx. It is distinguished from that species, however, by the stout, curved to uncinate trichomes almost all over the calyx, and the pedicels which are not erect and appressed to the flowering axis in the fruiting stage as in *M. stricta*, but are subhorizontal to reflexed.

The typical subspecies, which is distributed all over southern Europe and the Middle East differs markedly in the shape and size of its nutlets (as described above) from the plants of the species distributed in Afghanistan, West Pakistan, Kashmir, and the adjoining parts of USSR and India. Because these plants show a geographical isolation from the plant belonging to the typical subspecies, I have recognised them here as subspecies *chitralica*.

5. **M. alpestris** F. W. Schmidt, Fl. Boëm. 3: 26. 1794; M. Pop. Fl.

URSS 19: 377. 1953; Riedl in Rechinger, Fl. Iranica 48: 260. 1967.

M. silvatica Hoffm. subsp. *alpestris* Koch, Syn. Fl. Germ. 505. 1837.

TYPE: Habitat locis paludosis montium Iserae majoris fluvii, Sudetorum, sylvae Bohemicae, *F. W. Schmidt s.n.*

ICON.: Reichenb. Icon. Fl. Germ. 18: *t. 121.* 1856.

Perennial, caespitose herb. Stems usually many, erect to sometimes decumbent, simple to branched, to 30 cm. long, covered densely with white, crisped trichomes subappressed to appressed on the upper parts, spreading below, to 1 mm. long, usually tuberculate at base. Basal leaves petiolate, narrowly lanceolate, oblong or oblong-ovate, entire, obtuse, (including petiole) to 8 cm. long and 15 mm. broad, petioles usually longer, sometimes equalling the lamina, both surfaces covered sparsely or densely with slender, spreading trichomes to 1 mm. long, arising from tuberculate bases; cauline leaves sessile, linear, linear-oblong or linear-lanceolate, obtuse to subacute, to 2.5 cm. long, 5(–8) mm. broad. Inflorescence short, scorpioid in flower, later elongated, simple or branched, ebracteate. Pedicel short in flower, elongated in fruit to 5 mm., longer than the fruiting calyx. Calyx obviously narrowed towards the pedicel at base, divided to or below the middle, 1.5–2.5 mm. long in flower, to 3 mm. in fruit, lobes lanceolate, densely ciliate at margins, cilia long and acute, sparsely covered throughout with short, white, ± appressed trichomes, intermixed with long, stout, straight or (towards the base of the calyx) curved (and the lowermost sometimes uncinate) spreading trichomes. Corolla blue, tube ± equalling the calyx, limb 5–9 mm. in diameter, lobes roundish, spreading. Nutlets dark brown, smooth, shining, ovate, broadly obtuse at apex, apically and laterally margined in the upper half, ventrally slightly keeled near the apex, areola basal, horizontally compressed.

DISTRIBUTION: Europe, Asia, North America.

Myosotis alpestris is a very variable species of wide distribution. Vestergren (Arkiv Bot. 29A(8): 15–22. 1939) recognized many subspecies and varieties of *M. alpestris* represented in different geographical areas. In our area the following subspecies occurs:

Subsp. asiatica Vestergren in Hultén, Fl. Kamtchatka 4: 80. 1930; Arkiv Bot. 29a(8): 21. 1939.

TYPE: "Typus in Tomsk."

Subspecies *asiatica* is distinguished from the typical subspecies by the following characters: stems to 50 cm. tall; basal leaves linear-lanceolate to rarely oblong, obtuse, (including petioles) 3.5–5.5 cm. long, 3–10 mm. broad; pedicels to 5 mm. long in fruit; calyx divided nearly to the middle, stout and long trichomes on the calyx usually straight, sometimes curved, or rarely, with few uncinate ones on the lower portion of the calyx.

DISTRIBUTION OF SUBSPECIES: Arctic Europe and Asia, central Asia, Iran, Afghanistan, West Pakistan, Kashmir, northwestern India.

West Pakistan: CHITRAL STATE: Chitral Gol, west of Chitral, 3450 m., *Stainton 2693* (BM); Owir, 3450 m., *Bowes Lyon 886* (BM); Ziarat, 3000 m., *Harriss 16415* (K). GILGIT AGENCY: Baltistan, Satpura Nullah, ca. 4000 m., *R. R. Stewart 20264* (GH); upper Satpura Pass, ± 4000 m., *M. A. Siddiqui, Y. Nasir & Zaffar Ali 4230* (BM, RAW); Tsogosbang, above Barol Brok, right side of the Sospor glacier, *Schlagintweit 6100* (GH); above Dras, 3300–4000 m., *Duthie 13789* (K); Deosai Plains, 3900 m., *R. R. Stewart 20038* (GH, US); Karakoram-Haramosh Range, Mani Basin, *Culbert 3* (BM); Makerum, Hispar glacier, 4500 m., *Russell 1453* (BM), 3750–4500 m., *Russell 1428* (BM); Kero Lugma glacier, left bank, 4350 m., *Russell 1269, 1270* (BM); Zangia Harhar, Hunza Valley, 3900 m., *Russell 1024* (BM); Hispar glacier, right bank, E. of Sekarambarisi glacier, 3900–4500 m., *Russell 1523* (BM); Biafo Glacier, 4150 m., *Russell 1806* (BM, GH); Sokha glacier, right bank, 4500 m., *Russell 1621* (BM); Minapin glacier, 3450 m., SE. facing slope, *Lloyd & Megan 58, 59* (BM), ungrazed island in glacier, 3580 m., *Lloyd & Megan 72* (BM); Gharesa glacier, junction with glacier from Momhil Sar, 4740 m., *Polunin 6193* (BM), 12 miles east of Nagar, 3800 m., *Polunin 6265* (BM); by Burchi, bank of Gargo glacier, 2400 m., *Conway 6* (BM); Baltistan, without locality, 4200 m., *Hunter-Weston 10248* (MICH); without locality, in sheltered Nalas, 4200–4500 m., Pamir Boundary Commission, *Alcock 17744* (BM, K). HAZARA DIST.: Kaghan Valley, Babusar Pass, 3500 m., *Kazmi 2387b* (PES); Gittidas, *Shaukat Ali 124* (BM, RAW); Kaghan Valley, *Hassanud Din 103* (MICH). SWAT STATE: Bishgram, 3300–3600 m., *R. R. Stewart & A. Rahman 24964* (BM); without locality, *R. R. Stewart s.n.* (GH).

Kashmir: Burzil Pass, 3900–4200 m., *R. R. Stewart 22057, 22071a, 19864* (GH); Sonamarg, 3500 m., *R. R. Stewart 12550* (GH); Pir Panjal, 3300 m., July 6, 1876, *C. B. Clarke 28720A* (BM), Aug. 10, 1901, *Inayat* (K); Allyabad, Pir Panjal, *Inayat 25704* (K); Zanskar, Pensi La, 4950 m., *Koelz 5903* (GH, MICH, US), *5832, 5854* (GH, US); Rangdum, Zanskar, 4500 m., *Koelz 2921a* (GH, US), 4500 m., *Koelz 2921a* (GH); Zojibal, 3580 m., *Pinfold 312* (BM), Oct. 6, 1912, *Evershed s.n.* (BM); Hudan Valley, 3300 m., *Bellis in Gamble 1364* (K); Baltal in Sind Valley, 2700–3000 m., *Duthie 11590* (BM); above Trakbal, 3000 m., *Koelz 9199* (GH); Nuna Koi, 2450 m., *Pinfold 287* (BM); Pahlgam, 3000 m., *R. R. Stewart 9249, 8137* (GH); Kolohoi Valley, Sept. 1913, *Evershed s.n.* (BM); Ahbad, *C. B. Clarke 28888c* (BM); Rajdhiangan Pass, 3300 m., *R. R. Stewart 22552a* (GH); vicinity of Pahlgam, on east Lidder Valley, 27 road-miles north of Islamabad, *Dickason 77* (MICH).

From the typical subspecies the plants belonging to subspecies *asiatica* differ in being tall, lax, and having comparatively larger flowers. The plants within the subspecies *asiatica* are also very variable in the frequency of branching, form of leaves, and the composition of long and short trichomes on the calyx. The long and stiff trichomes on the calyx vary from straight to curved or, sometimes, even hooked at their tips. Most of the collections from West Pakistan and Kashmir do not bear any hooked trichomes, but plants with hooked trichomes are not rare. I have found hardly any specimens from the Middle East or Afghanistan lacking uncinate trichomes.

The very constant and distinct characters, which distinguish *Myosotis*

alpestris subspecies *asiatica* from the other species of our area are the form of the calyx and of the nutlet. The calyx in subspecies *asiatica* is narrowed towards the base with a long pedicel, and the nutlets are margined only on the upper half and apex, and are slightly keeled ventrally. The other species in our area with calyces attenuate at the base are *Myosotis stricta* and *M. refracta* which are distinguished by always having pedicels shorter than the calyx. *M. albicans* has nutlet more or less like subspecies *asiatica* but has white corollas and the calyx rounded at the base.

6. **M. albicans** Riedl in Rechinger, Fl. Iranica **48**: 261. 1967.

TYPE: West Pakistan: Swat, Utror, 2200 m., 6 June, 1965, *K. H. Rechinger 30826* (w-holotype).

ICON.: Riedl, l. c. *t. 43*. 1967.

Perennial (to biennial ?) subcaespitose herb. Stems solitary to many, erect, simple to branched, 5–25 cm. long, covered sparsely with spreading trichomes. Basal leaves petiolate, oblong-spathulate to oblong-ovate with rounded apex, petioles usually obviously shorter than lamina, (including petioles) 3–4 cm. long, 5–12 mm. broad, covered above with appressed and below with spreading, thick trichomes, arising from minute calcareous tubercles; lower cauline leaves subsessile to short petiolate, equalling the basal leaves; upper cauline leaves sessile, linear-lanceolate, 2–3 cm. long and 3–7 mm. broad. Inflorescence terminal, scorpioid, congested when young, becoming elongate, densely strigose with grayish, appressed trichomes. Pedicels erect, to 2 mm. long in flower, later spreading, nearly twice as long as the fruiting calyx, to 6 mm. long. Calyx divided nearly to the middle, to (1.5–)2.5 mm. long in flower, slightly elongated in fruit, to 3 mm., rounded at base, wide open above, lobes linear-lanceolate, covered below with large, often spreading, uncinate trichomes, and on the lobes with appressed to subappressed, straight to curved trichomes intermixed all over with short ones. Corolla white to bluish white, tube slightly shorter than the calyx, ca. 2 mm. long, limb spreading, 5–6 mm. in diameter. Style short, stigma capitate. Nutlets (only immature ones seen) broadly ovate, narrowly margined, obtuse, ca. 1.5 mm. long, areola small, sometimes slightly laterally drawn.

DISTRIBUTION: West Pakistan.

West Pakistan: SWAT STATE: Kalam, in cedretis, 2000 m., *Rechinger 30787* (w); Utror, 2200 m., *Rechinger 30826* (w-type).

7. **M. silvatica** Ehrh. ex Hoffm. Deutschl. Fl. **1**: 61. 1791; DC. Prodr. **10**: 107. 1846, excl. vars.; Ledeb. Fl. Rossica **3**: 145. 1847; Boiss. Fl. Orient. **4**: 237. 1875; M. Pop. Fl. URSS **19**: 373. 1953; Riedl in Rechinger, Fl. Iranica **48**: 258. 1967.

TYPE: In silvaticis umbrosis, *F. Ehrhart 31* (?).

ICON.: Hegi, Fl. Mitt.-Eur. 5(3): *fig. 3125*. 1927.

Biennial to perennial erect to suberect herb. Stems solitary to few, usually branched to sometimes simple, to 50 cm. long, covered sparsely or densely with white, crisped trichomes, to 1.5 mm. long, arising from minute tuberculate bases. Basal leaves petiolate, oblong-elliptic to oblong-lanceolate, entire, rounded or broadly obtuse at apex, gradually narrowed towards the base into petioles, to 6 cm. long, ca. 35 mm. broad, covered on both sides with trichomes, more or less resembling those on the stem; middle cauline leaves sessile, to 12 cm. long, 35 mm. broad; upper cauline leaves narrower and shorter. Inflorescence short in flower, later elongated to 15 cm. and bearing the fruiting calyces to 15 mm. apart. Pedicels short in flower, equalling or longer than the calyx in fruit. Calyx 1.5–2.5 mm. long in flower, 3–5 mm. long in fruit, divided 2/3 to 3/4 of its length, bases obviously rounded, lobes lanceolate, acute, spreading in fruit, densely covered with straight, curved or uncinate trichomes. Corolla blue, purple, or bluish white, to 10 mm. long, lobes roundish, spreading; faucal appendages well developed. Style equalling or shorter than the calyx. Nutlets blackish brown, ovoid, slightly and narrowly margined all around, acute, glabrous, smooth, shining, 1.5–2 mm. long.

DISTRIBUTION OF SPECIES: North Africa, Europe, Turkey, Iran, USSR, West Pakistan, Kashmir, northwest India.

The widely distributed species *Myosotis silvatica* is distinguished by Vestergren in his work, published posthumously by Stroh (Arkiv Bot. 29A(8): 1–39. 1938) in subspecies *frigida*, *cyanea*, *rivularis*, and *latifolia*. Stroh, in his note (*l. c.* p. 6), mentioned that Vestergren on the basis of his pollen investigations considered the plants, related to *Myosotis silvatica*, from western Himalayas, as a distinct species. For this species Vestergren (on herbarium sheets) gave the name *Myosotis himalaica*. As he did not give a botanical description or mention any characters distinguishing it from the other related species, the name remained a *nomen nudum*. Because I could neither examine enough material of *M. silvatica* from the other areas of its distribution, nor study the pollen morphology of the subspecies, I, therefore, list the plants from our area under subspecies *rivularis*, to which they are very closely related.

Subsp. **rivularis** Vestergren, Arkiv Bot. 29A(8): 12. 1938; Riedl in Rechinger, Fl. Iranica 48: 258. 1967.

TYPE: Taures cilicicus: Bulghar Dagh, in valle Su Nedere, *Kotschy 330* (w-lectotype).*

Differing from the typical subspecies by the following characters: Stems erect, flaccid, more heterophyllous than in the typical subspecies, to 35 cm. long; basal leaves lingulate, cauline leaves lingulate, broadly linear

* The lectotype is selected by J. Grau (Oesterr. Bot. Zeitschr. 110: 521. 1963).

to subovate, apiculate to obtuse; calyx divided nearly to the middle, to 4 mm. long in fruit, lobes narrow, acute, covered with numerous spreading to reflexed trichomes, those on the lower part uncinate; corolla 5–8 mm. in diameter; nutlets small, acute, obviously marginate, areola small.

DISTRIBUTION OF SUBSPECIES: Turkey, Armenia, Iran, West Pakistan, Kashmir, northwestern India.

West Pakistan: GILGIT AGENCY: Baltistan, environs of Skardu, 2000–2250 m., *Schlagintweit 835* (BM, GH). HAZARA DIST.: Kaghan Valley, between Shogran and Sari Rest House, ca. 2500 m., *Kazmi 2138* (PES); Naran, stony ground, *Jafri & Ali 3421* (BM).

Kashmir: Gulmarg, 2400–2700 m., *Duthie 13038* (BM), 2700–3300 m., *Barbour s.n.* (BM); vicinity of Sonamarg, on Sind River, 50 road-miles northeast of Srinagar, *Dickason 81* (MICH); Sonamarg, *R. R. Stewart 648.3* (K), 3300 m., *R. R. Stewart 12549* (GH), Aug. 11, 1921, *R. R. Stewart s.n.* (K); Aru Nafran, upper Lidder, 2700 m., *R. R. Stewart 12551* (GH); Fras Nag, Pir Panjal Range, 2700 m., *R. R. Stewart 23190* (GH, US); Rattan Pir, 2400 m., 4 July, 1876, *C. B. Clarke 28274A* (BM); Khelenmarg, 3240 m., *Polunin 56/264* (BM); 3000 m., *Polunin 56/135* (BM); Nowboog Valley, *Ludlow 29* (BM); Baltal in Sind Valley, ca. 3000 m., 26 June 1892, *Duthie 11590* (BM); Pir Panjal, 3250 m., 6 July 1876, *C. B. Clarke 28720A* (BM); Ahbad, ca. 3100 m., 6 July 1876, *C. B. Clarke 28888* (BM); vicinity of Pahlgam, on east Lidder River, 27 road-miles north of Islamabad, *Dickason 82* (MICH); without locality, 1915, *Prescott-Decie s.n.* (BM).

8. **M. arvensis** Hill, Veg. Syst. 7: 55. 1764.

TYPE: *Pl. 52, fig. 2, a,b,c*, Short leav'd Mouse Ear.

Annual or biennial herbs. Stems erect, usually many, to 35 cm. long, branched, branches slender, short to long, covered sparsely to densely with crisped, spreading trichomes to 1 mm. long, arising from tuberculate bases. Basal leaves petiolate, petioles shorter or longer than the lamina, lamina ovate, obtuse, 1–2 cm. long, to 10 mm. broad, covered on both sides with spreading to subappressed trichomes tuberculate at base; cauline leaves sessile, lanceolate, acute, gradually reduced upwards. Inflorescence simple, short in flower, later elongate, bifurcate, lax. Pedicels short in flower, equalling or longer than the calyx in fruit. Calyx divided to or below the middle, to 2 mm. long in flower, elongated to 3–5 mm. in fruit, lobes more or less incurved, holding the nutlets, densely covered all over with short, stiff, uncinate, spreading trichomes. Corolla blue to dark purple, campanulate, 2.5 mm. long, tube equalling or shorter than the calyx, limb ascending to spreading, 3–4 mm. in diameter, lobes roundish. Nutlets ovate, acute, narrowly margined all around, black, shining, areola minute.

DISTRIBUTION: Europe, N. E. Africa, Kashmir, W. Pakistan, India.

Kashmir: Burzil Pass, 3300–3900 m., *R. R. & I. D. Stewart 19018* (US); Sonamarg, 2700 m., *R. R. Stewart 2603* (K); northeast of Margan Pass, between Kashmir and Kishtwar, 2700–3300 m., 8 Aug. 1918, *Fuller 37* (K); Baltal.

Sept. 1880, *Young s.n.* (BM); Tragbal, *R. R. & I. D. Stewart 17958* (GH); vicinity of Pahlgam, on east Lidder Valley, 27 road-miles north of Islamabad, *Dickason 82* (MICH); Kishanganga Valley, Keran, 1500–2700 m., *R. R. & I. D. Stewart 17520* (GH); Khel to Taubat, 1950 m., *R. R. Stewart 17851* (GH); near Bhogtaur, 2280 m., *R. R. Stewart 17933* (GH). Miscellaneous: without locality, Herb. Late East India Co., *Falconer s.n.* (GH); Himal. bor. occ., regio temp., 6000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM, GH).

C. B. Clarke (in Hook. f. Fl. Brit. India 4: 173. 1883) refers these plants under *M. arvensis* Hoffm. Deutschl. Fl. 1: 85.

M. arvensis is closely related to *M. silvatica* from which it is distinguished by having smaller flowers, calyx more densely covered with uncinate trichomes, and smaller nutlets. At maturity the calyx lobes are not spreading but more or less incurved, holding the nutlets. Specimens of *M. arvensis* have slender stems more profusely branched than those of *M. silvatica*.

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TWO NEW SPECIES OF LEGUMINOSAE

G. P. Yakovlev

In continuing studies on the Leguminosae tribe Sophoreae, material of two previously undescribed species in the genera *Ormosia* and *Diplotropis* came to light. Both these taxa seem clearly distinct from their presumed close relatives. My purpose in describing them now is to bring them to the attention of collectors in the hope that new and more complete material will become available through future field activity.

I am glad to express my appreciation to the directors and curators of several institutions who were most generous in sending their material on loan for my studies. These include the herbarium of the Arnold Arboretum of Harvard University, Cambridge, Massachusetts (A); the herbarium of the Indian Botanic Garden, Howrah, Calcutta (CAL); the herbarium of the Department of Botany, Field Museum of Natural History, Chicago (F); the herbarium of the Department of Systematics and Plant Geography of the Botanical Institute of the Academy of Sciences of the USSR, Leningrad (LE); the herbarium of the Divisão de Botânica do Museo Nacional, Rio de Janeiro (R); the herbarium of the Department of Botany, University of California, Berkeley (UC); the herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (US).

Ormosia assamica Yakovlev, sp. nov. Arbor 25–30 m. alta; folia 7-foliolata, 3.2–3.7 dm. longa, petiolis circa 5 cm. longis, sparsim subtiliterque pubescentibus, foliolis oblongo-ellipticis vel late lanceolatis, apice aequabiliter acuminatis, basi truncatis, 10–15 cm. longis, 3.5–5 cm. latis, utrinque subglabris, nervis secondariis 10–12, prominulis, petiolulis ca. 0.5 cm. longis. Inflorescentiae appresse ferrugineo-pubescentes vel ferrugineo-villosae; flores 1.2–1.3 cm. longi, bracteolis jugatis deltoideis parvis, pedunculis ca. 0.5 cm. longis, calycibus 0.9–1 cm. longis, dentibus 0.5 cm. longis, corolla alba, petalis interioribus uniauriculatis. Legumen ignotum. — Figure 1.

Type: Assam. Akha Hills, Assam Valley. Dec. 1890. *Badul Khan 10* (CAL, holotype).

This new species is probably most closely allied to *Ormosia pinnata* (Lour.) Merr. and *O. robusta* (Roxb.) Baker. The holotype (CAL) and only specimen I have seen was determined previously as *O. robusta* from which it differs significantly, as it also does from other species from southern and southeastern Asia.

When fruit of *Ormosia assamica* is known it may be that its closest relationship will prove to be with those species having septate legumes,

FIGURE 1. **Ormosia assamica** Yakovlev. Holotype (CAL), *Badul Khan 10*.

which as a group I have recently included in a distinct new genus (Botanicheskij Zhurnal, in press).

FIGURE 2 (left). **Diplotropis duckei** Yakovlev. Paratype (A), *Ducke 64*. FIGURE 3 (right). **Diplotropis racemosa** (Hoehne) Amsh. Holotype (R no. 2901) *Kuhlmann 389*.

Diplotropis duckei Yakovlev, sp. nov. *Diplotropis racemosa* (Hoehne) Amsh. var. *parvifolia* Ducke, Legum. Amaz. Brasil. 104. 1939. Arbor; folia 15–17-foliolata, 7–8 cm. longa, foliolis oblongis basi oblique obtusis, supra glabris, subnitidis, subtus sparse appresse pubescentibus, 0.7–2.3 cm. longis, 0.4–0.9 cm. latis, petiolulis ca. 1 mm. longis. Inflorescentiae axibus appresse pubescentibus; flores 1–1.2 cm. longi, pedunculis 1–1.5 mm. longis, calycibus ca. 0.5 cm. longis. Fructus 1–2-sperma, planus, membranaceus, lanceolatus, 6–10 cm. longus, 1.4–2 cm. latus; semina oblonga, exalbuminata, testa tenui. — FIGURES 2 and 3.

TYPE: Brazil. Manáos, Estr. do Aleizo, *Ducke 1461* (LE, holotype; R, UC, US, isotypes); Manáos, *Ducke 64* (A, F, paratypes).

The new species, *Diplotropis duckei*, is most closely related to *D. racemosa* Hoehne from which it differs in the number and size of its leaflets and in the character as well as the size of many other parts, as shown in the table below.

	DIPLOTROPIS RACEMOSA	DIPLOTROPIS DUCKEI
LEAF	11–13(–15)-foliolate	15–17-foliolate
LEAFLETS	(1.4)1.7–3.8(4.5) × (1.1)1.4–1.9(2.3) cm.	(0.7)1–1.7(2.3) × 0.4–0.9 cm.
PETIOLULE	1.5 mm.	3–4 mm.
INFLORESCENCE	9–12 cm.	4–6 cm.
PEDICEL	3–4 mm.	1–1.5 mm.
CALYX	0.6–0.7 cm.	0.5 cm.

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LEONARD J. BRASS (1900–1971), AN APPRECIATION

LILY M. PERRY

ON AUGUST 29, 1971, with the passing of Dr. Leonard J. Brass in Cairns, Queensland, the scientific world lost one of its most kindly and unselfishly co-operative members. He first visited the Arnold Arboretum after the Nederlandsch Indische-Amerikaansche Expeditie (Third Archbold Expedition, 1938–39) to West Irian (then Netherlands New Guinea). This was a co-operative expedition "carried out with the assistance and collaboration of the Netherlands Indies government, which provided a military covering party and part of the scientific personnel." As far as results were concerned, perhaps this was the largest of the Archbold Expeditions. Mr. Brass made 5,532 numbered collections on it, amounting to almost 34,000 sheets of specimens. This was the first time I had met him, although I had processed his Fly River Expedition specimens. I handled his collections from four Expeditions in all and kept in contact with him. It seems appropriate therefore, to mention a few of my memories.

It was a joy both to process and to study Mr. Brass's collections. The packages were so trim that one would think he had sheared the edges before wrapping them; the specimens were well chosen, ample, and beautifully prepared; his collection data were both extensive and meticulous. He took great pains with his field notes, and he wanted to see them used. The report on his Fly River palms was published without the long, detailed (and I may add, necessary) field notes. "Didn't you send my field notes with the study set?" "Yes, Mr. Brass." "Since they weren't published, will you please see that the data are sent out in full with each duplicate set?" Another time a German worker published "See Daviumbo" for Lake Daviumbu (I had seen the proof of the article but was not permitted to change the German spelling), so Mr. Brass called this spelling to my attention thinking that a mistake had been made in the preparation of the label. I simply said, "I will show you the master label, the one sent was a carbon copy [which was correct!]"

He seemed to be able to remember vividly every plant he had collected and the place he got it. One day I happened upon a single small plant with a beautiful blue flower lying near the edge of a sheet of some monotone umbellifer. He was working at the next table in the herbarium. As all the plants were strange to me, I wasn't trying to remember what I had seen, but I didn't want to discard anything precious, so I said, "How could you mix two plants like these under one number?" He immediately came to look at the plants, drew a small field book out of an inside pocket, looked over a couple of pages, and said, "Try this number."—It belonged there, but had slipped out of order. Then he told me about the

place he had found it, and as he described the surroundings it seemed as if he could see every plant in place.

He was an excellent photographer. When we talked about this part of his work he said, "The secret is to take your pictures early in the morning when everything is still." One anecdote he told on himself was that one morning about 9 o'clock he found a tree which he wanted to photograph but the wind was already beginning to rise. After trying several angles for his camera, the gusting wind spoiling each view, he became annoyed; "Then," he said, "my boys [helpers] hid behind the trees and laughed at me."

Another time I asked him if it was difficult to get along with the natives. His reply was: "Only once I was in trouble. After emerging from the forest I saw a row of *Pandanus* trees — one had a cluster of fruits hanging. I shot off the cluster. A native came running, and he was very angry, so I offered him the fruits and told him I didn't know I shouldn't. Of course a crowd gathered, and I learned that *Pandanus* was sacred to them and this row had been planted. However, after much talk we parted and I was more careful afterward."

Then I asked about the head-hunters. From his pocket he drew a chain with a charm attached; it was small, made of tiny feathers, a bit of fur and other things. He said that it was a charm for protection. "How did you get that," I asked. "When you go into the wilds where you have to be your own doctor, you must know how to take care of yourself if you should become ill. I exchanged some of my know-how with the witch doctor." Incidentally, in connection with cannibalism he told the wife of a staff member who had invited him to dinner, "Some of the Papuans would love you." She was very plump.

He had the keenest interest in his collections and the work which was being done on them. If any identifications came in they were to be reported to him promptly. Just as he had worked hard to get the specimens into the hands of botanists, he expected them to do as much to put the results into his, but he helped in every way that he could. Many times when I had questions about habitats, I received a prompt and clear explanation of what I needed to know. One time he told me, "I was too late to get help from Corner's monkeys and a bit early for access to the field by airplane," — so he had had to make collections the hard way, coping with many difficulties. He said that in the field it was very monotonous to get along without any green food. Sometimes they took care of that difficulty by using palm cabbage, but on the third expedition mentioned above, he had made a wrong guess and all those who ate it were poisoned by *Orania* cabbage. His illness was most violent and on the next day he was still too weak and shaken to get about.

When we were so busy amalgamating the herbaria of the Arnold Arboretum and the Gray Herbarium, I was a very long time turning in a report on his plants collected on the 4th Archbold Expedition and was feeling apologetic for the delay. His reply was, "In this matter of getting

LEONARD J. BRASS at Baniara (Milne Bay Div., Papua), 2 May, 1953. *Photo. R. D. Hoogland.*

things done, I used to think any persons interested in their job ought to be able to work eight days a week. I still do mostly six days, plus some night time. But . . . I have to admit that I can't get as much done as I used to . . . even though conscious weight of years (almost 61 of them) is something I have had no cause to bother about so far."

In 1965, Mr. Brass sent me (and Dr. van Steenis) a summary of the numbers, general localities, time, and place of deposit of his collections, approaching 35,000 in number. But he was not only a collector, he was also a naturalist and a brave explorer. His consideration of others perhaps may be illustrated by the following: after he returned from one expedition on which another member of the staff (a zoologist) had suffered a stroke, he took over his collections and processed them for him at the American Museum of Natural History. I said, "How difficult when he couldn't talk." His reply was, "I watched his eyes; I knew him well enough to read approval or disapproval in the expression of his eyes." When the last expedition went to New Guinea (while he was still living in this country but unable to go along) he took care of making all the arrangements and of hiring whenever possible Papuan helpers he had already trained on earlier trips. His mind was never very far from New Guinea.

We remember his charming smile, the interest with which he greeted us, his readiness to help, his remarkable capacity for work and his complete devotion to it. Those of us who knew him and the scientific world are the poorer by his going.

Arnold Arboretum
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